
THE XOCHIXTLAPILCO DINOSAUR ICHNOFAUNA, MIDDLE JURASSIC OF OAXACA, SOUTHEASTERN MEXICO: DESCRIPTION AND PALEONTOLOGIC SIGNIFICANCE

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ABSTRACT. The Xochixtlapilco Dinosaur Ichnofauna was recovered from fine-grained, red phyllarenitic strata of the Middle Jurassic Tecocoyunca Group *partim*, which was laid down in a coastal lagoon, and dated as Early Bajocian–Early Bathonian on the basis of ammonites. The site lies in the Oaxacan Mixteca, southeastern Mexico. The ichnofauna chiefly consists of small footprints, whose makers are referred to as a “basal coelurosaur” (Morphotype A tracks); an undescribed sauropod taxon, probably of family rank (Morphotype C tracks); and an ankylopollexian ornithopod (Morphotype D tracks). There is also a single large footprint made by an ?allosaurid carnosaur (Morphotype B track). This small but relatively diverse ichnofauna is the southernmost record of Jurassic dinosaurs in North America, and adds a new fauna to the meager record of dinosaurs in Middle America.

During the Jurassic the Mixteca territory (≈Mixteca Terrane) was one of several small continental-crust blocks laid down in the inter-American/African space, as Pangea became disassembled. Ecologically such a scenario corresponded to an isolated setting where limited space and resources might have induced selective pressures toward small size, especially to the primary consumers and associated predators; it also shielded the island fauna from competition and exchange with neighboring continental faunas. Nonetheless, the Xochixtlapilco dinosaur fauna shows a closer biogeographic/phylogenetic resemblance to the North American faunas than to the South American or African faunas; however, the meaning of this fact can not be fully ascertained at present because of the Xochixtlapilco fauna’s small size.

RESUMEN. La Dinosauricnofauna Xochixtlapilco fue recolectada de estratos rojos, finogranudos filareníticos del Grupo Tecocoyunca *partim*, depositados en una laguna costera, y fechados como bajocianos tempranos-batonianos tempranos, con base en amonitas. El sitio se encuentra en la Mixteca Oaxaqueña, sureste de México. La icnofauna principalmente consiste de huellas podiales pequeñas, cuyos autores son referibles a un “celurosaurio basal” (huellas del Morfotipo A), a un taxon no descrito de sauropodo, probablemente de rango de familia (huellas del Morfotipo C), y a un ornitópedo ankylopollexiano (huellas del Morfotipo D); también hay una sola huella grande, hecha por un carnosaurio ?allosáurido (huella del Morfotipo B). Esta pequeña, pero relativamente diversa icnofauna es el registro más austral de dinosaurios jurásicos en Norteamérica, y agrega una nueva icnofauna al escaso registro de dinosaurios en Mesoamérica.

Los modelos de tectónica de placas sobre la evolución geológica/tectónica de Mesoamérica, presentan al territorio Mixteco (≈Terreno Mixteco) durante el Jurásico, como uno de los pequeños bloques de corteza continental dispuestos en el espacio interamericano-africano, a medida que Pangea se desmembraba. Ecológicamente tal escenario correspondía a un marco isleño, donde lo limitado del espacio y recursos, pudieron haber inducido presiones de selección hacia tamaño pequeño, especialmente en los consumidores primarios y en los depredadores asociados a ellos; dicho escenario protegió a la fauna isleña de competencia e intercambio con faunas continentales vecinas. Sin embargo, la dinosauriofauna Xochixtlapilco muestra un mayor parecido biogeográfico/filogenético con la fauna norteamericana que con la sudamericana o la africana; al presente, sin embargo el significado de este hecho no puede establecerse aún, debido al pequeño tamaño de la fauna Xochixtlapilco.

INTRODUCTION

The Mesozoic tetrapod faunas of temperate North and South America and Europe are

somewhat better known than those of Asia and Africa. The Jurassic assemblages have a high percentage of shared taxa, which in turn suggests land connections that allowed migration of taxa

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and/or geographic extension of faunas. However, the detailed Jurassic paleogeography and the tetrapod faunas of southern North America and of the middle American/Caribbean region are very poorly known. The Mexico record is based mainly on Late Cretaceous faunas north of the Trans-Mexican Volcanic Belt (TMVB). Location of the chief continental Mesozoic tetrapod faunas of Mexico are plotted in Figure 1 and listed in Table 1.

To properly evaluate the faunistic relationships between North and South America, it is critical to have a large database on the Mexican Mesozoic, particularly the Jurassic tetrapod record. An added benefit of this database is that it poses objective constraints on the paleogeographic and tectonic models proposed to depict the complex geologic evolution of the middle American-Mexican region during the Mesozoic. In this paper, the Xochitlapilco Dinosaur Ichnofauna, Middle Jurassic of Oaxaca, southeastern Mexico (Figure 1 (Ferrusquía-Villafranca et al., 1995)), a small, but important, footprint assemblage from a locality south of the TMVB, is described in full, and its regional significance discussed, as a contribution to increase the meager dinosaur database of the Mexican-middle American region. Further, it is essential to monograph this ichnofauna now, before it becomes irretrievably lost to erosion within a few years because of the frailness of the footprint-bearing rock strata.

A preliminary study of the site was conducted in 1981 by Mr. Oscar Comas, then teaching in the Facultad de Ciencias, Universidad Nacional Autónoma de México (UNAM) (Comas and Applegate, 1982). Visiting the site when the footprints were less weathered, he made plaster casts of several footprints and deposited them in the Museo de Paleontología of that school; these casts were lent to the senior author by Dr. Pedro García-Barrera, Curator of the Museo. Mr. Comas also furnished two tracing-paper silhouettes of footprints (IGM-9309 and IGM-9310), as well as measurements of some prints. All the material is deposited in the Colección Nacional de Paleontología, Instituto de Geología, UNAM (acronym IGM used for formal cataloguing).

The general patterns of vertebrate locomotion and its functional anatomical design generate a limited number of basic configurational patterns reflected in the dinosaur footprints. Therefore, similarity of footprint morphology discloses only a generalized degree of taxonomic affinity, usually no lower than family level. The taxonomic value of footprints is real but limited, because both biological and nonbiological factors introduce variables that affect footprint morphology. Among the biological factors, the most significant one is the pedal/manual anatomy of the individual that made the prints. In turn, this anatomy is modified by individual variation (sex, age, size, etc.), and locomotory and behavioral aspects

(standing, resting, stalking, walking or running, being solitary or gregarious, etc.).

The nonbiological factors mainly pertain to the nature and to the later geological history of the strata bearing the footprints. The nature of the stratum determines the precision and quality of the prints. The diagenesis and later history of the track-bearing strata also influence the print quality. Such considerations lead us to take a conservative approach and limit our taxonomic identifications to the family level at most.

MATERIAL, METHODS, AND TERMINOLOGY

The footprints lie on a hill slope formed by steeply tilted red sandstone strata with few clear exposures. The footprint-bearing strata were in most places too friable to attempt removal or casting of prints, so there is no direct material record of them. During visits to exposed areas by the senior author, each individual print was numbered and measured. To record the relative position and spacing of the prints, they were carefully delineated in full size with indelible ink markers on transparent plastic sheets placed over the outcrop.

Three sequences were recorded: IGM-7958, a 4-m-wide and 6-m-long sheet with 34 footprint silhouettes from the main outcrop; IGM-7960, a 1-m-wide and 1.5-m-long sheet with three footprint silhouettes from a smaller outcrop located 20 m east of the main one; IGM-3006, a 0.8-m by 0.8-m square sheet with a single footprint silhouette from another small outcrop located about 80 m east from the main one. From the latter a plaster cast was made (IGM-3006).

In an effort to detect the orientation of the prints when they were made, the plastic sheet was properly oriented both topographically and structurally. The structural restoration of the strata to the original horizontal position allows one to establish the orientation of the prints with respect to the present-day North Pole. This information could then be transferred to the Middle Jurassic North Pole position inferred from paleomagnetic data of the Mixteca region (cf. Caballero-Miranda et al., 1991).

Epi-relief/hyporelief casts pairs were made from the epi-relief cast suite of the Facultad de Ciencias, UNAM (IGM-9303/-9304, IGM-7428/-9305, IGM-7430/-9306, IGM-9311/-9312, IGM-9313/-9314, and IGM-7425/-9315). A photographic record was made of the casts and plastic sheets. The description of each track, as well as the shape and numerical parameters used, follows Peabody (1948), Sarjeant (1975), Ferrusquía-Villafranca et al. (1978), and Lockley (1991b).

We adhere to the usage of Thulborn (1989:41) for the following terms: small theropods are those whose average footprint length is less than 25 cm, large theropods are those whose average footprint length is more than 25 cm; small ornithopods are

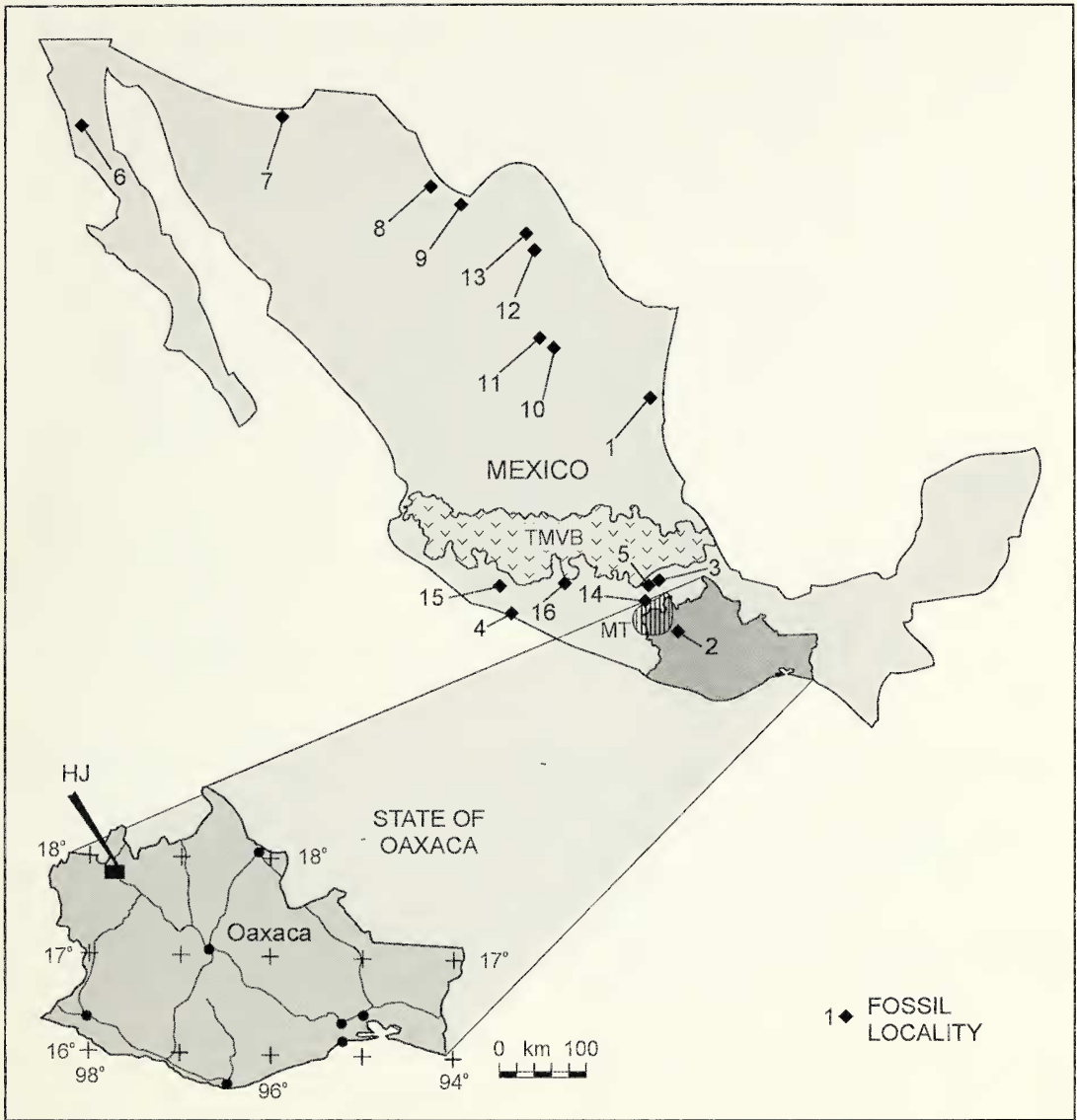


Figure 1 Index map of Mexico showing the location of the chief continental Mesozoic tetrapod faunas (1–14), the TMVB, and the Mixteca Terrane (MT). The state of Oaxaca (southeastern Mexico) is blown up to show the position of the study area (HJ, Huajuápan de León Area, Mixteca Alta region). **Faunas:** Early Jurassic, Tamaulipas State: 1, Huizachal Fauna. Middle Jurassic, Oaxaca State: 2, Xochitlapilco Dinosaur Ichnofauna. ?Middle/Late Jurassic, Puebla State: 3, Otlaltepec single occurrence. Late Jurassic, Michoacán State: 4, Chuta Dinosaur Ichnofauna. Early Cretaceous, Puebla State: 5, San Martín Atexcal Dinosaur Ichnofauna; Late Cretaceous, Baja California State: 6, El Rosario Fauna. Sonora State: 7, Cabullona Faunule. Chihuahua State: 8, Ojinaga single occurrence. 9, Altares faunule. Coahuila State: 10, El Pellillal Fauna. 11, Rincón Colorado Fauna. 12, Sabinas Dinosaur Ichnofauna. 13, Palau single occurrence. Puebla State: 14, Mitepec Dinosaur Ichnofauna. Michoacán State: 15, El Aguaje Dinosaur Ichnofauna. 16, Tiquicheo single occurrence

those whose average footprint length is less than 25 cm, large ornithopods are those whose average footprint length is more than 25 cm. It should be noted that the qualifiers large(er) and small(er) are sometimes used as comparative terms and related to the known or inferred adult size of the taxon under consideration; this usage is clearly deduced from the context. Other terms and

measurements used, as well as the corresponding abbreviations, are illustrated and spelled out in Figure 2.

The nomenclatural treatment adopted in this paper is based on the concept and usage of morphotypes and morphic varieties. Sarjeant (1992:304) also recommends that the names of ichnotaxa should be based upon ichnofossil

Table 1 Major Mesozoic tetrapod faunas of Mexico

Period	State	Fauna
Early Jurassic	Tamaulipas	Huizachal Fauna (Clark et al., 1994)
Middle Jurassic	Oaxaca	Xochitlápilco Dinosaur Ichnofauna (Comas and Applegate, 1982; Ferrusquía-Villafranca et al., 1995, 1996, this study).
?Middle/Late Jurassic	Puebla	Otlaltepec (Applegate and Ferrusquía, unpublished information)
Late Jurassic	Michoacan	Chuta Dinosaur Ichnofauna (Ferrusquía-Villafranca et al., 1978; Tilton et al., 1996)
Early Cretaceous	Puebla	San Martín Atexcal Dinosaur Ichnofauna (Rodríguez-de la Rosa et al., 2004)
Late Cretaceous	Baja California	El Rosario Fauna (Morris, 1967, 1972, 1973)
	Sonora	Cabullona Faunule (Lucas and González-León, 1990, 1993; Taliaferro, 1993)
	Chihuahua	Ojinaga single occurrence (Ferrusquía-Villafranca, unpublished information)
		Altares Faunule (Andrade-Ramos et al., 2002)
	Coahuila	El Pellilal Fauna (Rodríguez-de la Rosa and Cevallos-Ferriz, 1998, Rodríguez-de la Rosa, 2003)
		Rincón Colorado Faunule (Kirkland et al., 2000)
		Sabinas Dinosaur Ichnofauna (E. Jimenez-Hidalgo, unpublished information)
		Palau single occurrence (Ferrusquía-Villafranca, unpublished information)
	Puebla	Mitepec Dinosaur Ichnofauna (Ferrusquía-Villafranca et al., 1993)
	Michoacan	El Aguaje Dinosaur Ichnofauna (Ortiz-Mendieta et al., 2000)
		Tiquicheo single occurrence (Benammi et al., 2004)

morphology, not on the presumed affinities of the trace maker. Much the same is advocated by Lockley (1989:441) and by Farlow et al. (1989:385), who strongly recommend that formal names should be given only to dinosaur tracks preserved well enough to provide significant information about the pedal structure of their maker. Thus, given the small number of available ichnites and their moderate to poor preservation, we have chosen not to assign formal ichnogenetic names to them but rather to refer to them as morphotypes and morphic varieties. However, in an effort to tie morphotypes to known ichnogen-
era, we discuss the relevant ichnotaxonomic record.

A morphotype is the fundamental configuration of an ichnite that allows it to be differentiated from other such configurations and constitutes an informal taxonomic category; in this paper, however, morphotypes are given a capital letter designation. Morphotype makers can confidently be linked to family categories of the Linnean system. Morphic varieties (MV) document variability within a given morphotype. In this paper, morphic varieties are designated with the corresponding morphotype capital letter, followed by a particular lowercase letter, thus producing a unique two-letter combination. These categories are also informal. The possible Linnean taxonomic identification of the morphotype maker is discussed; the assignment made, usually a category of family or higher rank, is the most parsimonious estimate on the basis of the morphological information, known biogeochronologic ranges,

and geographic distribution of the taxa involved. Inevitably, given the current extensive usage of cladistic analysis of skeletal remains to characterize and work out the phylogenetic relationships of generic and higher-rank dinosaur taxonomic categories, some of the names referred to in this study are now cladistically defined, but still remain Linnean taxonomic categories, and are named accordingly. We use and refer to such categories as taxonomic/nomenclatorial “handles” to convey the possible taxonomic position of the morphotype maker, and certainly no cladistic analysis of bone remains is implied.

GEOLOGICAL SETTING AND
PALEOGEOGRAPHIC CONSIDERATIONS

GEOLOGIC SYNOPSIS OF THE HUAJUAPÁN
DE LEÓN AREA, OAXACA

The dinosaur footprint locality lies in the Mixteca Alta Oaxaqueña, Municipality of Huajuapán de León, northwestern Oaxaca State, southeastern Mexico, 17°42'–17°50'N Lat. and 97°45'–7°52'W Long. (Figure 2). The area includes nearly 160 sq. km of rugged, complexly deformed territory, where Paleozoic to Quaternary units crop out (Figures 3 and 4). The Paleozoic Acatlán Complex in the Mixteca region is unconformably overlain by the Jurassic System, which largely consists of a 1,700- to 2,500-m-thick, sedimentary, continental-to-marine sequence; its current lithostratigraphic differentiation (Erben, 1956a and b, Cortés-Obregón et al., 1957) into two

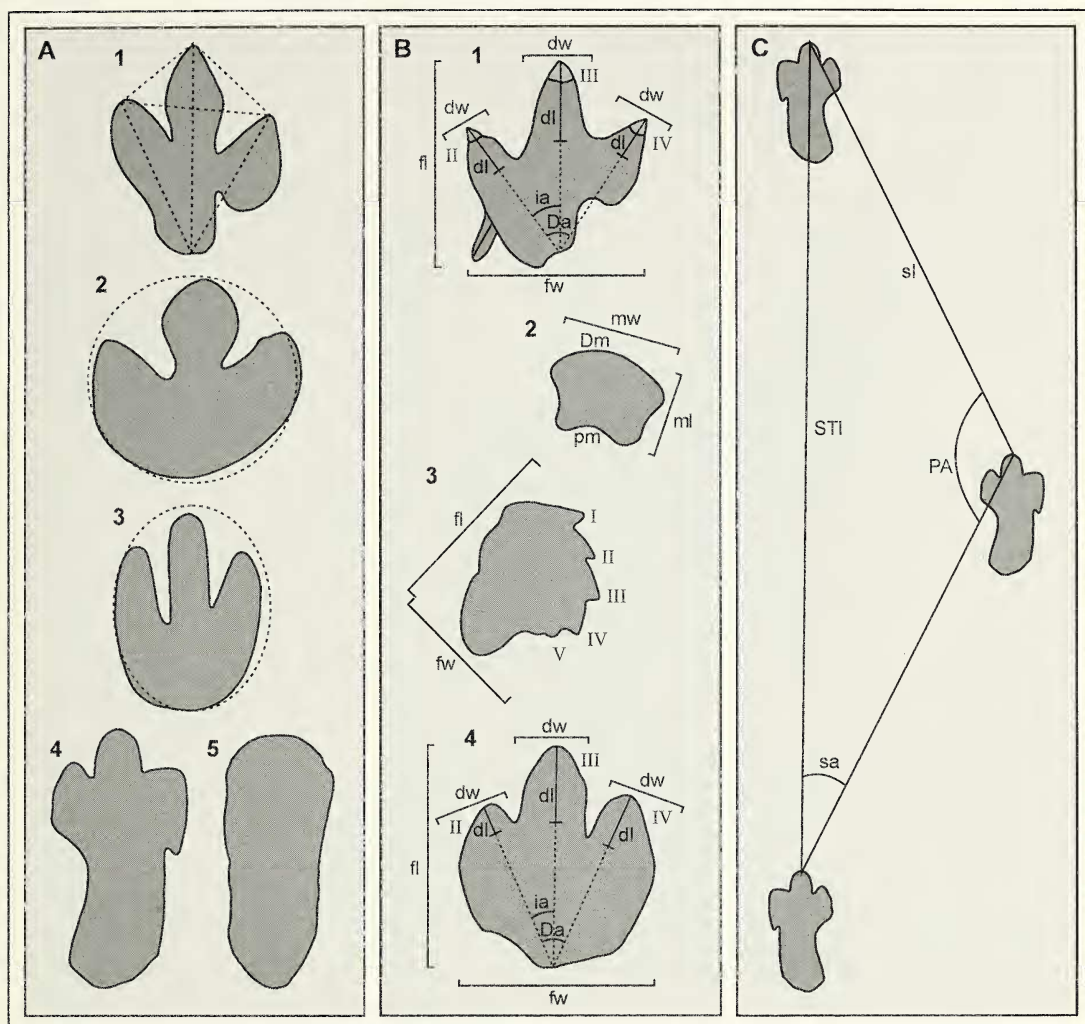


Figure 2 Descriptive track and trackway terminology used (modified from Peabody (1948), Sarjeant (1975), Ferrusquía-Villafranca et al., (1978), and Lockley (1991b)). A1–A5: track shapes of A1, rhomboidal; A2, rounded; A3, oval; A4–A5, hyperelongated; the interdigital notch is V-shaped in A1 and A3 and U-shaped in A2; B1–B4: track measurements of B1, theropod footprint; B2–B3, sauropod pedal and manual prints respectively; B4, ornithopod footprint. ABBREVIATIONS: Da, divergence angle; dl, apparent digit length; Dm, dorsal margin (of manual print); dw, width of digit at its base; fl, antero-posterior footprint (= pedal print) length; fw, transverse footprint (= pedal print) width; ia, interdigit angle (between stated digits); ml, antero-posterior length of manual print; mw, transverse width of manual print; pm, palmar margin (of manual print); C trackway measurements; PA, pace angulation; sa, step angle; sl, step length; STI, stride length

groups (the Early Jurassic Consuelo Group and the Middle to early Late Jurassic Tecocoyunca Group) and eight formations needs a thorough revision (not attempted here) because the recognition of the formations beyond their type areas is uncertain or altogether impossible due to their lithic resemblance and complex structural deformation.

In the study area (Figures 3 and 4), the footprint bearing strata belong to the Tecocoyunca Group *partim* (i.e., an undifferentiated lithostratigraphic unit of group rank, where only some of the formations that make it up are present). This

group is a fine to medium-grained, phyllarenitic clastic body, largely laid down in a transitional environment, and corresponds to a huge delta complex. About 18 km S 8°W of the dinosaur footprint locality (see Figure 3), in the Diquiyú-Rio Santa Catarina 'subarea', Taberna Formation strata (a largely clastic, shallow marine and transitional unit of the Tecocoyunca Group) located above the dinosaur footprint-bearing beds contain ammonites such as *Duashnoceras floresii* Burckhardt, 1927, *Subcollina lucretia* d'Orbigny, 1847 (Sandoval and Westermann, 1986), *Strigoceras* (*Lyroxinites*) cf. *S. (L.) kellumi* Imlay, 1961,

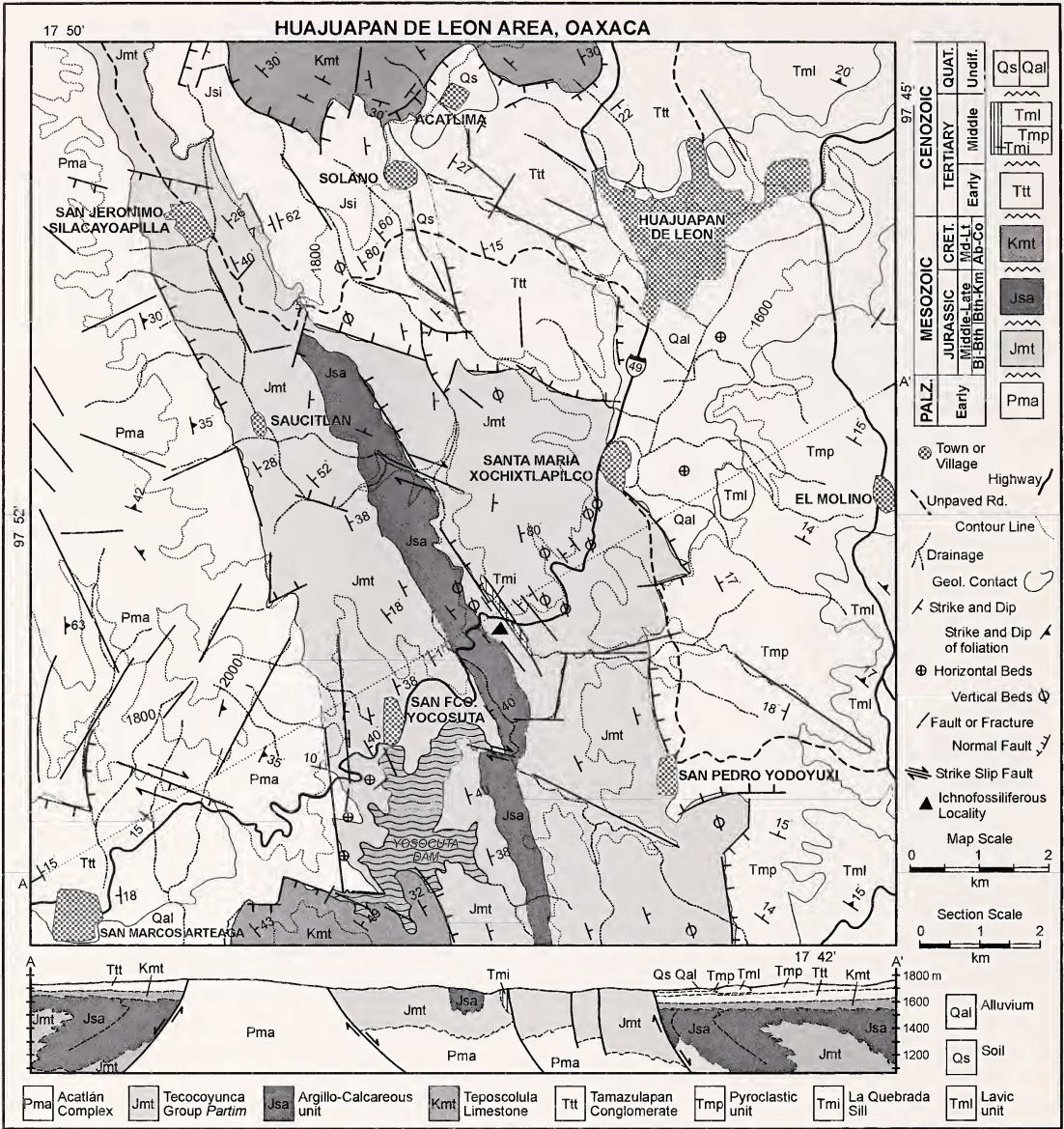


Figure 3 Geologic map and structural section of the Huajuapán de León Area, Mixteca Alta, Oaxaca, and southeastern Mexico

Lissoceras cf. *L. oolithicum* d'Orbigny, 1845 (Sandoval and Westermann, 1986), *Oppelia subradiata* Westermann, 1983, *Parastrenoceras zapotecum* Ochoterena, 1963, and *Stephanosphinctes buitroni* Sandoval and Westermann, 1986 (Erben, 1956a; Sandoval and Westermann, 1986), that indicate an Early Bajocian–Early Bathonian age. In the study area, poorly preserved plant remains referred to as *Otozamites* sp. (Silva-Pineda, 1984) are present; their geochronological range is congruent with the Middle Jurassic age assignment obtained from the ammonites. The structure of the Tecocoyunca Group *partim* in the area includes two north-northwest–south-southeast trending,

complexly and tightly folded anticlinoria, separated by a narrow synclinorium (Figure 3). Normal faulting further complicates the structures. The dinosaur footprint-bearing strata are located near the western edge of the eastern anticlinorium, where a thin basaltic andesite sill intrudes the sequence. The textural and primary structural features of these strata, such as laminar to thin bedding, ripple marks, immature fine grain sandstones, siltstones, and claystones, indicate that they were deposited very probably on the shores of a coastal lagoon.

The Tecocoyunca Group *partim* is overlain by a Late Jurassic marine unit, in turn overlain by the

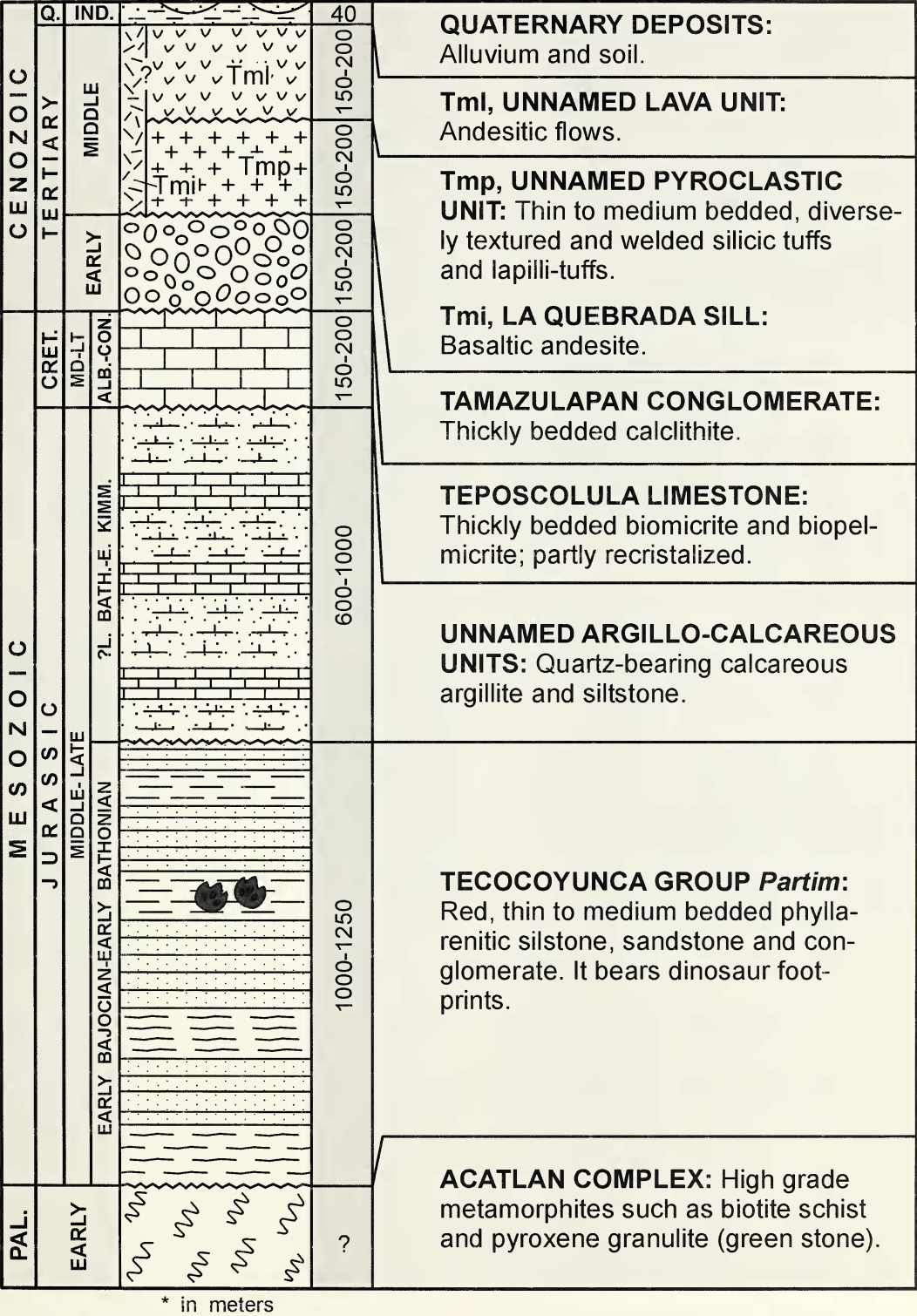


Figure 4 Generalized lithostratigraphic column of the Huajuápan de León Area, Mixteca Alta, Oaxaca, and southeastern Mexico

Albian Teposcolula Limestone, which is overlain by a Cenozoic continental sequence (Figures 3 and 4).

PALEOGEOGRAPHIC CONSIDERATIONS ON THE MIXTECA REGION

The Mixteca is part of the southeastern Mexico–middle American–Caribbean region, whose geologic evolution during the Mesozoic is far from well known. Several competing models of tectonic and/or paleogeographic evolution have been proposed (see Anderson and Schmidt, 1983, for a review of early models). Figure 5 depicts six such models proposed (between 1988 and 2004) for the Jurassic. Notice that all of them include several small continental-crust blocks lying in the space left between North America, South America, and Africa as Pangea became disassembled. Paleogeographically they corresponded to islands. However, there are not enough data to positively constrain the sea/land boundary for any of them during any particular time interval (nor for the adjacent continents either). Later, some such blocks accreted to North America, generating southeastern Mexico–Central America, or formed the Greater Antilles. The Mixteca is one or part of one of these blocks.

There have been three studies on the paleogeographic and tectonic evolution of the Mixteca region (which is one, or part of one such blocks) during the Middle Jurassic, both based on paleomagnetic data. Caballero-Miranda et al. (1991: 206–209) considered two paleogeographic hypotheses. In one the Mixteca was located in the Southern Hemisphere, perhaps by the Central Andes (~20°S Lat.). This hypothesis was proposed by Westermann et al. (1984), Taylor et al. (1984), and Sandoval and Westermann (1986) to explain the close affinities of the Mixtecan and Andean ammonite faunas and implies at least a 37° northward rotation (i.e., about 4,500 km) from a starting position by present-day northern Chile.

In the second hypothesis the Mixteca was located in the Northern Hemisphere, around today's west-central Sinaloa (about 20°N Lat. and 108°W Long.), as advocated by Scotese et al., (1979), Anderson and Schmidt (1983), and Urrutia-Fucugauchi (1984), among others, who postulated a left lateral displacement related to the Sonora–Mojave and TMVB megashears. This hypothesis implies an oblique (southeastward, ~1,000 km) rotation from a starting position located 8° farther north and 10° farther west of the present-day location. However, the data to support this hypothesis (Caballero-Miranda et al., 1991: table 2) locate the Middle Jurassic Reference Paleomagnetic Pole at 61°N Lat. and 116°E Long., whereas the rotated Middle Jurassic Paleomagnetic Pole's location varies from 53° to 62°N Lat. and 144° to 165°E Long., thus calling for a much greater rotation (ca., 15° to 30°)

than the one proposed; nonetheless, Caballero-Miranda et al. preferred the second hypothesis.

Böhenl (1999) proposed a third hypothesis, namely a 25° southward post-Bajocian translation of the Mixteca from a starting position in northern South America across northeastern North America (i.e., by present-day New York, then located just south of the Paleoequator (Figure 5.4)).

In these hypotheses, the Mixteca region is regarded as an island located close to west-central South America (first hypothesis), close to southwestern North America (second hypothesis), or close to northeastern North America/northern South America (third hypothesis). The largely undifferentiated Pangeatic nature of the Middle Jurassic dinosaur fauna as a whole (Weishampel, 1990; Russell and Bonaparte, 1997; Sues, 1997a) lends no support to any of these hypotheses. However, the island component of all three hypotheses is consistent with the ecologic and geographic scenarios proposed for the Xochitlapilco ichnofauna towards the end of this article.

SYSTEMATICS

This ichnofauna is named for the village of Santa Maria Xochitlapilco, which lies 4.5 km southeast of the locality by Highway 49, segment Huajuapán de León–San Marcos Arteaga (Figure 3). The locality lies on an east–west trending, ~80-m-long, steep slope formed by brick red, laminar, phyllarenitic silty-clayey strata dipping 62° south-southeast (Figure 6); the average height of the slope is 8 m, and the footprints occur on bedding planes within a strata thickness no greater than 45 mm, hence they are regarded as contemporaneous. Close to the western end of the slope, there is a well-exposed bedding plane covering 16 m², where 33 footprints of small theropods and sauropods are present (Figures 6 and 7). About 20 m east of this main exposure, there is a much smaller one, where only three small ornithopod footprints (and a digit impression) are discernible (Figure 7). Farther east, close to the end of the slope, on its lower part, there is a single, large, well-preserved theropod print. The footprints of the latter exposures and some of the main outcrop are faintly outlined and shallow, which suggests that they are erosional remnants of true prints or underprints.

Order Saurischia Seeley, 1888

Suborder Theropoda Marsh, 1881

Coelurosauria, Huene, 1914,
sensu Holz et al., 2004

“Basal Coelurosauria” *sensu* Holz et al., 2004
Morphotype A, Morphic Varieties Aa to Ak
(Figures 8.1–8.4, Tables 2–3)

DESCRIPTION. Small, rhomboidal to oval tridactyl footprints; with short to moderately long

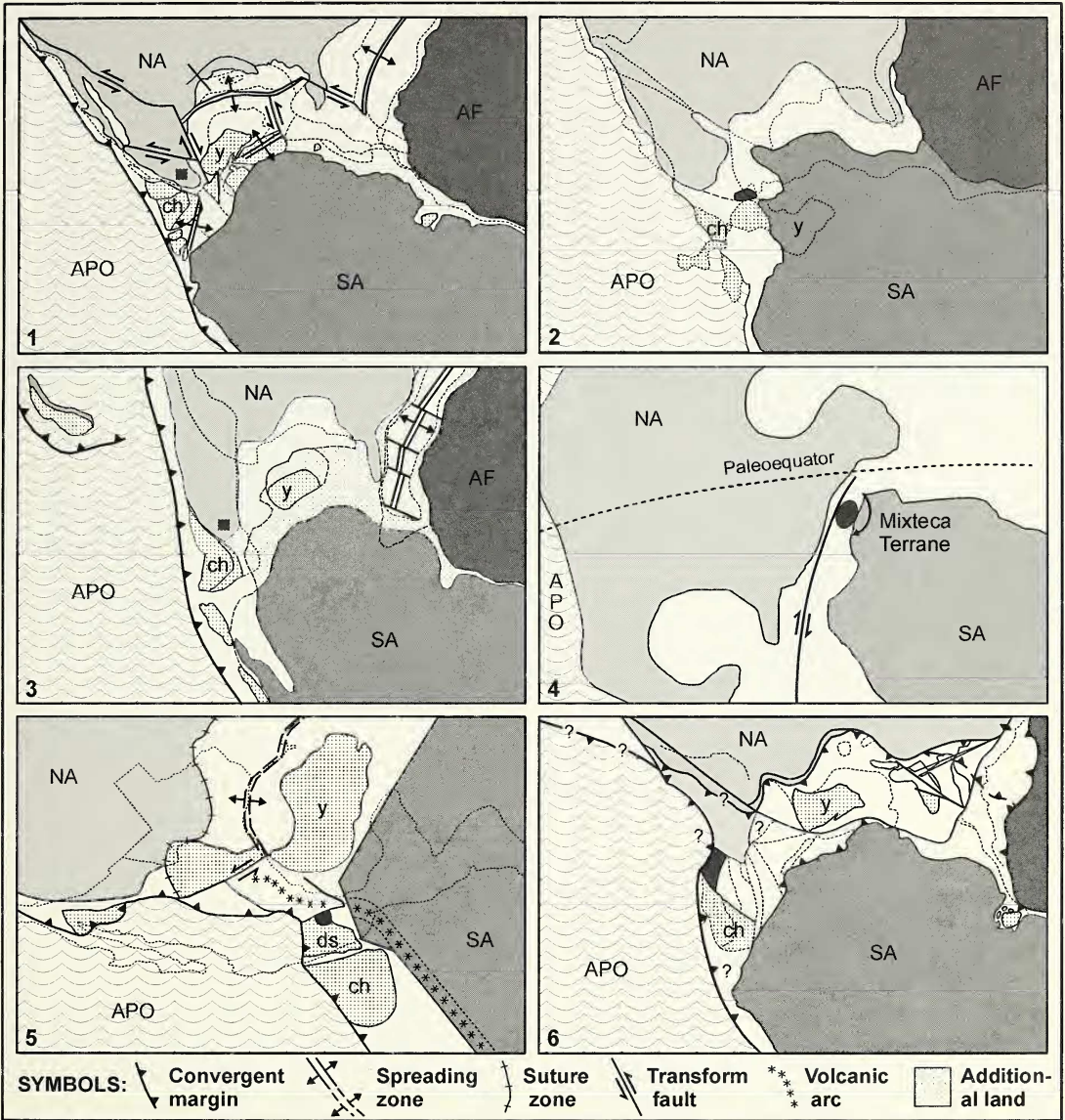


Figure 5 Paleogeographic and paleotectonic hypothetical reconstructions of the North American–South American–African region during the Jurassic, after 1, Ross and Scotese, 1988; 2, Smith et al., 1994; 3, Golanka et al., 1996; 4, Böhnelt, 1999; 5, Dickinson and Lawton, 2001; 6, Elías-Herrera, 2004 (all are slightly modified); notice that only some continental-crust blocks are labeled; the Mixteca Terrane Block is shown in solid black. ABBREVIATIONS: AF, Africa; APO, Ancestral Pacific Ocean; ch, Chortis Block; ds, Del Sur (i.e., Sierra Madre del Sur) Block; NA, North America; SA, South America; y, Yucatán Block

and robust digits separated by V-shaped notches, digit III is the longest and the others are subequal; divergence angle (between digits II–IV) typically of 54° to 78°, angle interdigits II–III of 39°–42°, and angle interdigits III–IV of ~20°–39°; estimated hip height of 0.50 m to 0.70 m; other numerical parameters are presented in Tables 2 and 3. Sixty percent of the recorded footprints are hyperelongated, seemingly combining the dactylar/plantar impression with a large metatarsal impression into a single print, which has

a humanlike footprint appearance because the pedal/metatarsal margin is diffuse. Eleven morphic varieties are recognized for this morpho-type.

Morphic Variety Aa

REFERRED MATERIAL. Plaster and plastic epirelief/hyporelief cast pairs numbers IGM-9303, IGM-9304 and IGM-7428, IGM-9305 (Figures 8.1Aa1P, 8.1Aa1N, and 8.1Aa2P, 8.1Aa2N); both correspond to left footprints.

Table 2 Measurements of footprints assigned to Morphotype A. ABBREVIATIONS AND SYMBOLS: aiII–III, angle between interdigits II–III; aiIII–IV, angle between interdigits III–IV; DA, divergence angle; dl, digit length; dw, width at digit base; e, estimated; fl, antero-posterior footprint length; fw, transverse footprint width; f#, number of footprints recorded in IGM-7958; I, indeterminate; H, hip height; L, left; MV, morphic variety; Mw, apparent maximum footprint transverse width; R, right; TPL, apparent maximum antero-posterior footprint length; (4), (6), casts made from these footprints in 1981. (A), morphometric ratio method: $h = 4.5 \text{ fl}$ (Thulborn, 1990:251, Equation 8.2); (B), allometric equation method: $h = 3.49 (1.5 \text{ fl})^{1.02}$ (Thulborn, 1990:255, Equation 8.15. Linear measurements in mm

f#	Side	MV	TPL	Mw	fl	fw	H		DA	ai	ai	dl	dw	dl	dw	dl	dw
							(A)	(B)		II–III	III–IV	II	II	III	III	IV	IV
–	L	Aa1	–	–	130	119	585	693	78°	39°	39°	65	24	72	25	58	24
–	L	Aa2	–	–	100	83	450	533	56°	42°	14°	30	22	52	28	30	17
–	L	Ab	–	–	120	77	540	640	45°	15°	20°	32	18	50	22	35	17
–	R	Ac	130	80	110	80	495	587	54°	30°	24°	44	16	60	13	–	13
–	R	Ad1	210	84e	–	–	–	–	60°	30°	30°	44	24	63	28	63e	21
–	R	Ad2	125	53e	–	–	–	–	56°	33°	23°	23	19	33	18	32	19
(6)	L	Ae	195e	78e	–	–	–	–	–	–	–	–	18	44e	13	42e	14e
(4)	L	Af	200e	85e	–	–	–	–	–	–	–	45e	20	68	23	–	18
–	L	Ag	205	78	122	74	–	–	–	–	–	–	–	–	–	–	–
9	L	Ah	260	130	125	124	–	–	–	–	–	–	–	–	–	–	–
15	L	Ai	–	150	–	133e	–	–	–	–	–	–	–	–	–	–	–
31	R	Ai	295	122	128	126e	–	–	–	–	–	–	–	–	–	–	–
2	L	Aj	295	126	–	121	–	–	–	–	–	–	–	–	–	–	–
10	I	Aj	–	110	–	110	–	–	–	–	–	–	–	–	–	–	–
16	R	Aj	315	125	–	123	–	–	–	–	–	–	–	–	–	–	–
29	L	Aj	328	130	–	129e	–	–	–	–	–	–	–	–	–	–	–
1	R	Ak	215	110	–	–	–	–	–	–	–	–	–	–	–	–	–
3	R	Ak	260	140	–	–	–	–	–	–	–	–	–	–	–	–	–
4	L	Ak	265	120	–	–	–	–	–	–	–	–	–	–	–	–	–
5	R	Ak	200	140	–	–	–	–	–	–	–	–	–	–	–	–	–
6	L	Ak	270	135	–	–	–	–	–	–	–	–	–	–	–	–	–
12	L	Ak	300	123	–	–	–	–	–	–	–	–	–	–	–	–	–
13	R	Ak	230	112	–	–	–	–	–	–	–	–	–	–	–	–	–
22	R	Ak	205	110	–	–	–	–	–	–	–	–	–	–	–	–	–
23	L	Ak	256	115	–	–	–	–	–	–	–	–	–	–	–	–	–
24	R	Ak	256	143	–	–	–	–	–	–	–	–	–	–	–	–	–
25	L	Ak	294	143	–	–	–	–	–	–	–	–	–	–	–	–	–

DESCRIPTION. They are small, rhomboidal to oval, have well-developed, moderately long digit impressions, with acute apices, which suggests the presence of narrow, elongated claws, digit III is the longest, a divergence angle of 56°–78°, angle interdigits II–III of 39°–42° and angle interdigits III–IV of 14°–35°; one of the footprints is slightly larger, with straight digits; the other has curved, shorter digits (particularly II and IV). The plantar portion of the footprint is little developed; no pads and heel impressions are discernible.

Morphic Variety Ab

REFERRED MATERIAL. Plaster and plastic epirelief/hyporelief cast pair number IGM-7430 and IGM-9306 (Figures 8.1AbP and 8.1AbN); it corresponds to a left footprint.

DESCRIPTION. This morphic variety is also small, with well-developed, acute-tipped digit impressions, which suggests the presence of claws, but differs from MV Aa in having narrower, nearly straight digits, with their tips slightly bent; the divergence angle of 45° is much smaller than in MV Aa, and so are the interdigit angles (15°

between II and III, and 20° between III and IV). Another difference is that the plantar region is larger, but no heel or pad impressions are discernible.

Morphic Variety Ac

REFERRED MATERIAL. Plaster and plastic epirelief/hyporelief cast pair number IGM-9307 and IGM-9306 (Figures 8.2AcP and 8.2AcN); it corresponds to a right footprint.

DESCRIPTION. This morphic variety is broadly similar to MV Aa (divergence angle of 54°), differing from it in being smaller, with rather thick, rounded-tipped digit impressions, and in possessing a long and narrow, posteriorly directed projection, interpreted as a metatarsal impression.

Morphic Variety Ad

REFERRED MATERIAL. IGM-9309 and IGM-9310, two silhouettes outlined in 1981 over tracing paper on a now-eroded part of the lower trackway (see Figure 7, and in “General Discussion of the Morphotype,” Morphotype Assign-



Figure 6 Photograph of the main outcrop of the Tecocoyunca Group *partim*, where most of the dinosaur tracks are exposed; black stripes are asphalt stains. This outcrop is what remains of a much larger bedding plane exposure that extended ~80 m to the east (right-hand side of the picture). The site is a road cut in Highway 49, located 6.3 km nearly due south of Huajuápan de León, Oaxaca. The square delimits the space illustrated in Figure 7; the bar on the lower part measures 1 m

ment section, number 2), Figures 8.2Ad1 and 8.2Ad2; both correspond to right footprints.

DESCRIPTION. Both footprints are very similar, but one is 50% shorter and ~37% narrower than the other; the digits are moderately long and have a broad base and acute tips, such as those of MVs Aa and Ab; digit II is shorter than digit IV, which is nearly as long as digit III; the divergence angle is ~58°; the angle between digits II and III is slightly greater than that between digits III and IV. The plantar region is broad and shows a posteriorly directed projection, interpreted as a metatarsal impression.

Morphic Variety Ae

REFERRED MATERIAL. Plaster and plastic epirelief/hyporelief cast pair number IGM-9311 and IGM-9312 (Figures 8.2AeP and 8.2AeN); it corresponds to a left print.

DESCRIPTION. This morphic variety has a hyperelongated outline and shows two distinct regions: the dactylar/plantar region makes up the anterior third, it is wider but shallower than the rest of the footprint; the digit impressions are nearly parallel, that of digit II is longer and wider than those of digits III and IV, which are successively shorter; the plantar portion is small, not well defined, shows no pads or heel impressions. The remaining two-thirds are narrower and

deeper and correspond to a large metatarsal impression; no discontinuity separates the plantar from the metatarsal impressions, so that the whole track has a human footprint-like appearance.

Morphic Variety Af

REFERRED MATERIAL. Plaster and plastic epirelief/hyporelief cast pair number IGM-9313 and IGM-9314 (Figures 8.3AfP and 8.3AfN); it corresponds to a left footprint.

DESCRIPTION. This morphic variety is ~15% longer and wider than MV Ae, but otherwise similar; it differs from it in having the digit II impression much shorter and that of digit III much longer, that is, it has the opposite condition that of MV Ae. MV Af is shallower, and has a wider and shorter metatarsal region (which makes up the posterior half of the footprint) than MV Ae.

Morphic Variety Ag

REFERRED MATERIAL. Plaster and plastic epirelief/hyporelief cast pair number IGM-7425 and IGM-9315 (Figures 8.3AgP and 8.3 AgN); it corresponds to a left footprint.

DESCRIPTION. This morphic variety is deep, hyperelongated, and relatively narrow; the dactylar/plantar region makes up ~60% of the whole print; the digit impressions are long and wide

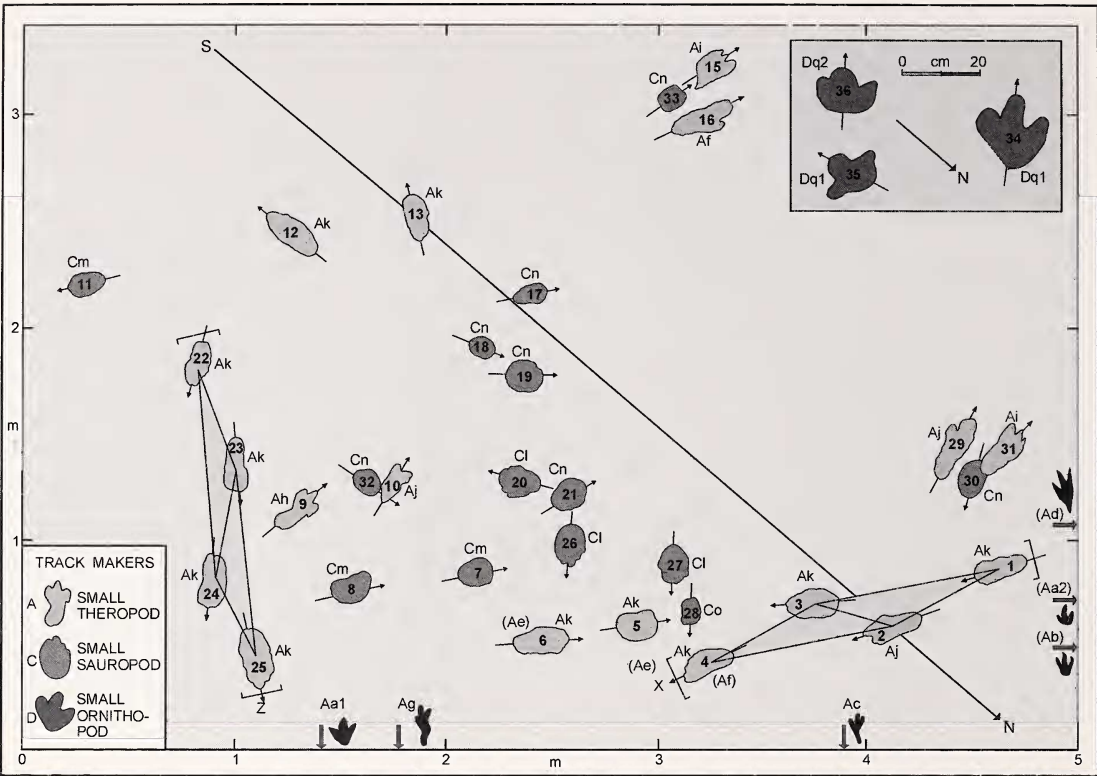


Figure 7 Sketch plane of the main outcrop of the Tecocoyunca Group *partim* depicted on Figure 6, showing the spatial distribution of the dinosaur footprints. The inset, upper right, corresponds to another (smaller) outcrop of the same track-bearing strata, located 20 m east of the main one. The capital-lowercase letter labels on each track indicate the morphotype (A, C, or D) and morphic variety to which it belongs (see text for description). The arrows denote the antero-posterior axes of the prints, the arrow heads point to the anterior end. The numbers inside the tracks correspond to those registered on the plastic sheets IGM-7958 and 7960. The N-S line represents the present-day north-south direction, after the structural restoration of the strata to their original horizontal position. The unnumbered footprint dark silhouettes located on the lower and right-hand-side margins correspond to plaster casts made in 1981, from tracks set on now-eroded parts (indicated by the dark arrows) of the main outcrop. The letters in parentheses (Ae) and (Af), refer to plaster casts also made in 1981, which still remain, but are much deteriorated. The narrow X and Z rhomboids correspond to trackways.

(especially so that of digit III), the angle between digits II–III is slightly narrower than that between digits III and IV; the plantar portion is small, showing no discernible pad or heel. The metatarsal region of the print is narrow, and joins the dactylar/plantar region at an oblique (~160°) angle, as if the digit/plantar region would have been laterally displaced some 20° off the straight metatarsal-plantar/digit III axis.

Morphic Variety Ah

REFERRED MATERIAL. IGM-7958, plastic sheet, impression number 9, which corresponds to a left footprint (Figure 8.3Ah).

DESCRIPTION. In this morphic variety, the dactylar/plantar region is wider than the metatarsal one; it has three short digit impressions on the anterior margin; that of digit III is longer and wider. The recess or notch between digits II and III is much narrower than that between digits III

and IV. The posterior half of the print corresponds to the metatarsal impression.

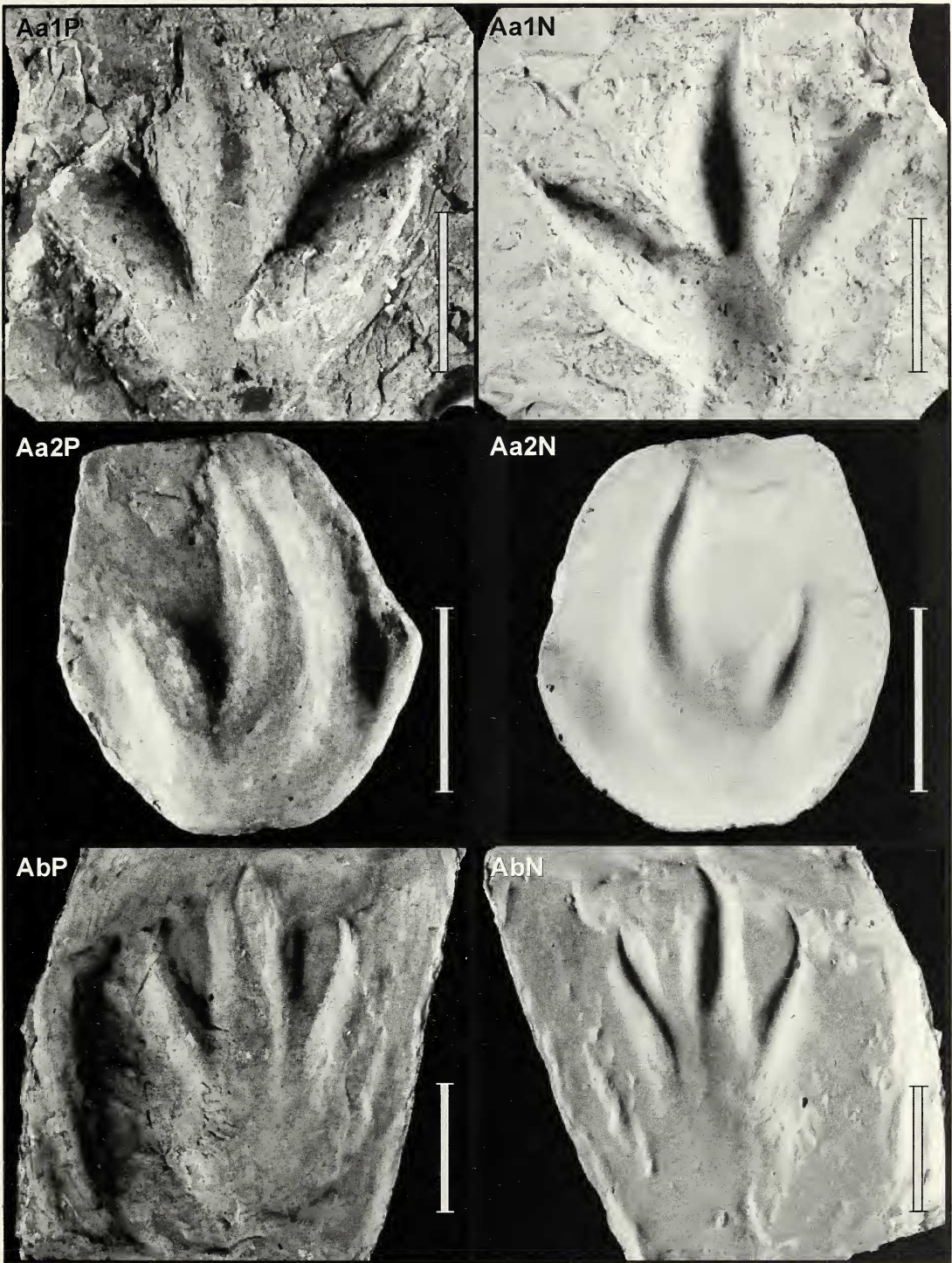
Morphic Variety Ai

REFERRED MATERIAL. IGM-7958, plastic sheet, impression numbers 15 (left, incomplete, only the anterior half remains) and 31 (right, partly overprinting a sauropod footprint, Figure 8.3Ai).

DESCRIPTION. This morphic variety is similar to MV Ah, but the dactylar/plantar region is less well defined, and has on the anterior margin three short, uneven digit impressions: that of digit II is wide and subround, the one of digit III is the longest, its tip is acute, and that of digit IV is barely visible. The posterior half of the footprint corresponds to the metatarsal impression.

Morphic Variety Aj

REFERRED MATERIAL. IGM-7958, plastic sheet, impression numbers 2 (left), 10 (indetermi-



Figures 8.1–8.4 Morphotype A, footprint assemblage originated by trackmakers referred to the “Basal Coelurosauria” *sensu* Holtz et al., 2004, scale bars = 5 cm. 8.1, morphic varieties Aa and Ab; Aa1P and Aa1N, photographs of IGM-9303, epirelief (P) and IGM-9304, hyporelief (N) casts of a left footprint; Aa2P and Aa2N, photographs of IGM-7428, epirelief (P) and IGM 9305, hyporelief (N) casts of a left footprint; AbP and AbN, photographs of IGM-7430, epirelief (P) and IGM-9308, hyporelief (N) casts of a left footprint

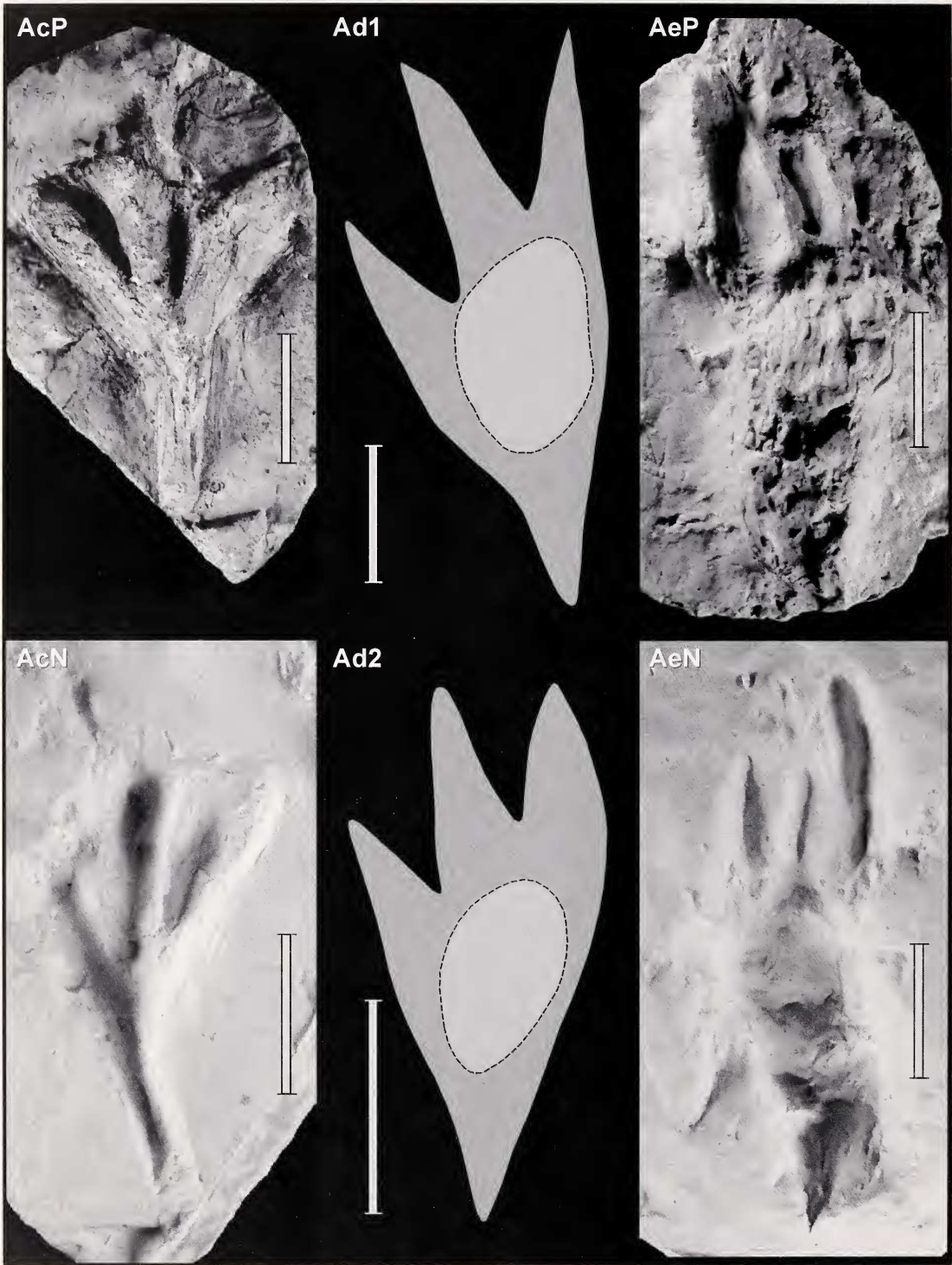


Figure 8.2 Morphic varieties Ac, Ad, and Ae; AcP and AcN, photographs of IGM-9307, epirelief (P) and IGM-9308, hyporelief (N) casts of a right footprint; Ad1 and Ad2, computer drawings of IGM-9309 and IGM-9310 respectively, silhouettes of right footprints taken directly from the main outcrop in Oaxaca; AeP and AeN, photographs of IGM 9311, epirelief (P) and IGM-9312, hyporelief (N) casts of a left footprint

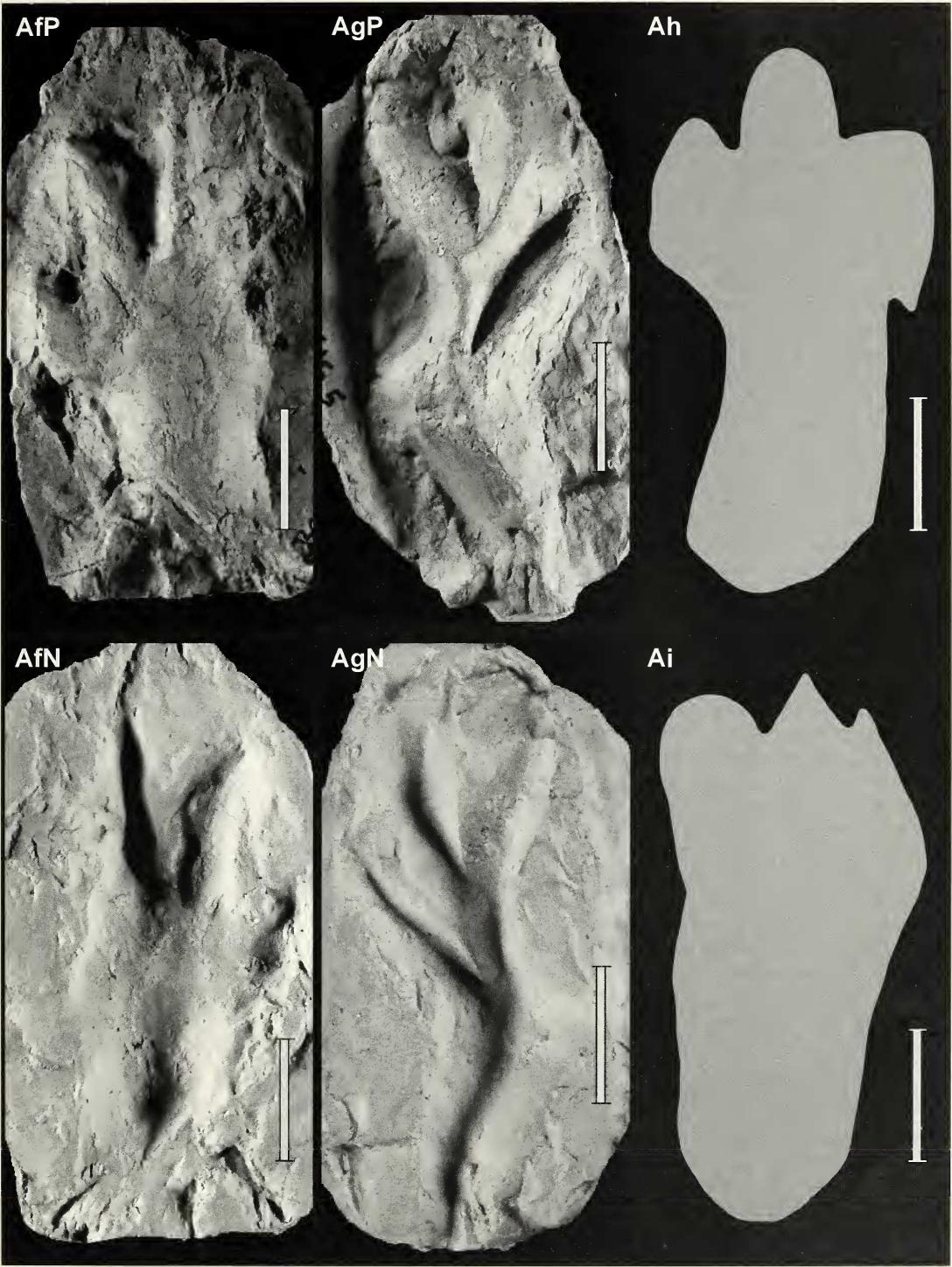
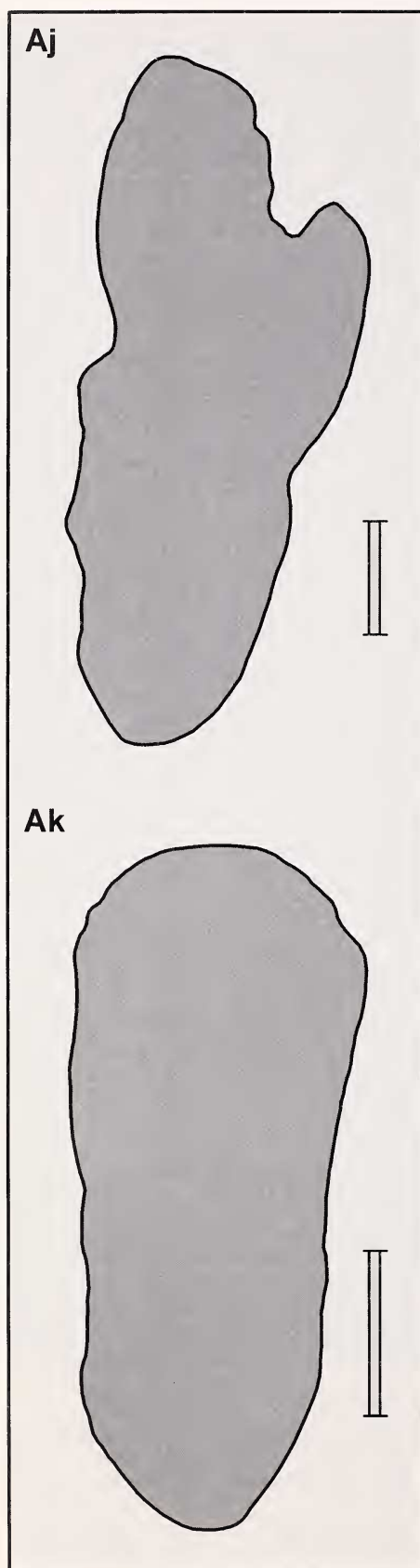


Figure 8.3 Morphic varieties Af, Ag, and Ah; AfP and AfN, photographs of IGM-9313, epirelief (P) and IGM-9314, hyporelief (N) casts of a left footprint; AgP and AgN, photographs of IGM-7425, epirelief (P) and IGM-9315, hyporelief (N) casts of a left footprint; Ah and Ai, computer drawings of selected footprint silhouettes (f# 9, left and f# 31, right respectively) from IGM-7958, plastic sheet outline record of footprints exposed on the main outcrop; (f# = footprint number)



nate, nearly complete), 16 (right, Figure 8.4Aj), and 29 (left).

DESCRIPTION. This morphic variety resembles MV Ai, differing from it in having a shallow constriction on the internal and external margins of the footprint, as well as a large anterior lobe (interpreted as the joint digits II and III impressions), separated by a shallow recess from a smaller lobe (interpreted as the digit IV impression). The posterior half of the footprint corresponds to the metatarsal impression.

Morphic Variety Ak

REFERRED MATERIAL. IGM-7958, plastic sheet, impression numbers 1, 3, 5, 13, 22, and 24 (right ones), impression numbers 4, 6, 12, 23, and 25 (left ones; Figure 8.4Ak).

DESCRIPTION. About 60% of the Morphotype A footprints belong to this morphic variety. Although the most frequent, it is the least typical of all, with an ellipsoidal hyperelongated outline, and no digit prints. It is interpreted that this odd, humanlike track shape corresponds to the combined dactylar/plantar and metatarsal impressions, as discussed in "General Discussion of the Morphotype," Morphotype Assignment section, number 2.

MV Ak includes the footprints that form the two trackways present in the main outcrop (cf. Figure 7 and Table 3). Trackway X lies in the lower right part of the outcrop. It consists of four footprints directed S 55°W with respect to the present-day North, the motion was from northwest to southeast. The stride length is 92 cm, the pace angle is 135°, and the step angle varies between 18° and 27°. Trackway Z lies in the lower left part of the outcrop, being nearly vertical. It is directed N 60°E, the motion was from southwest to northeast. The stride length varies from 92 cm to 103 cm, the pace angle ranges from 135° to 145°, and the step angle is similar to that of Trackway X.

GENERAL DISCUSSION OF THE MORPHOTYPE

Morphotype Assignment

The 20 footprints assigned to this morphotype show considerable diversity in shape, and less so in size, but in a grading fashion between end-size (smallest/largest) and end-shape (typical theropod/atypical theropod), which suggests that the track makers belonged to the same population, being just a small sample of it. Elsewhere, sets of footprints showing different morphologies (age-, gender-, individual variation-, preservation-, or deforma-

←

Figure 8.4 Morphic varieties Aj and Ak; computer drawings of selected footprint silhouettes (f# 16, right and f# 12, indefinite respectively) from IGM 7958, plastic sheet outline record of footprints exposed on the main outcrop; (f# = footprint number)

Table 3 Measurements of trackways ABBREVIATIONS AND SYMBOLS: PA, pace angulation; Sa, step angle; SI, step length; STI, stride length; Xf# = footprint numbers of trackway X; Zf# = footprint numbers of trackway Z. Linear measurements in cm

Measurements	Xf#	Data	Zf#	Data
SI	1–2	56	22–23	50
SI	2–3	40	23–24	56
SI	3–4	58	24–25	42
STI	1–3	89	22–24	98
STI	2–4	90	23–25	92
PA	2	135°	23	145°
PA	3	135°	24	140°
Sa	1	18°	22	18°
Sa	2	27°	23	18°
Sa	4	18°	25	25°

tion-related), have already been confidently assigned to a single theropod taxon (Breithaupt et al., 2003, 2004). The size spectrum (Tables 2–3) includes ‘little’ individuals interpreted as juveniles which as expected, are less numerous than the ‘big’ ones interpreted as adults. It should be noted though, that the actual footprint length might have been at least 25% longer because the plantar region of the prints seems to be not fully preserved, thus appearing less well developed than typical small theropod footprints (contrast Figures 8.1 and 8.2 with those of Lull, 1953:figs. 37–39; Lockley, 1991b:fig. 3.6; Thulborn, 1990:figs. 6.8–6.9). If morphotype tracks are indeed incomplete, their makers were larger and taller than implied by the dimensions reported in Table 2.

The morphic spectrum involves prints that grade from the typical tridactyl theropod footprints (MV Aa) to the atypical, hyperelongated, digitless, human footprint-like tracks (MV Ak), which makes up 60% of the entire sample. The gradational footprint shape changes illustrated by MV Aa through MV Ak were accomplished by incorporating more of the metatarsal impression to the footprint, and by the concomitant reduction and eventual deletion of the dactylar impressions. Because of the great departure from the typical theropod track morphology, MVs Af to Ak are in fact extramorphological variants. There could be three alternate reasons for this mode of locomotion:

1. The trackmaker was crouched, stalking prey in such a way that the weight was borne by the metatarsal, leaving a deep impressions of this bone, whereas the digits remained retracted, barely (if at all) touching the ground. However, digit retraction is unlikely, because the theropod foot structure allows a great deal of contraction, but very little or no retraction. Further, the presence in the same bedding plane of two differently oriented and directed trackways (made with this kind of footprints, see Figure 6), would indicate concurrent prey stalking, which seems unlikely.
2. The track maker had adopted a semiplanti-grade gait to provide support while walking over

slippery and/or soft, unconsolidated ground. The resulting prints would be deep, have a well-marked metatarsal impression, but sediment collapse around the footprint margin would have selectively destroyed small structures such as the digit impressions. These features are present to a varying degree in MV Ac to MV Ak, thus lending credence to this hypothesis. This second interpretation calls for the odd configuration of MV Ae through MV Ak to have resulted from a particular activity of the theropod track maker, rather than reflecting an unusual foot structure. Further, the configuration of each variety reflects the firm to slippery conditions of the substrate, as well as the hardness/softness of the sediment. Finally, the weathering and erosion after exposure reduce the footprint quality, producing changes in their shape and size and eventually deleting them. (Eight years after their discovery, no footprints of the MV Aa through MV Ag remained.)

3. The track maker could be walking on substrata of different firmness, which is inversely related to their degree of wetness, as shown by Gatesy et al. (1999). They studied a suite of Late Triassic small theropod tracks from Greenland. The suite displays a morphic spectrum that varies from typical tridactyl tracks to atypical, hyperelongated tracks with a large metatarsal impression and a digit I impression much longer than in typical tracks, thus producing a shape not unlike that of MV Ag (cf. Gatesy et al., 1999:figs. 1e–f; Figures 8.3AgP and 8.3AgN). They interpreted the spectrum as being made by theropods belonging to the same taxon but walking upon grounds of different firmness. Experimental studies of turkey and helmeted guinea fowl walking on substrata differing in firmness and wetness show that the track shape changes from typical to atypical as the wetness increases, thus supporting their interpretation.

Comparison between Gatesy et al., 1999:figs. 1a–f, and this work, Figures 7.1AaP–7.1AaN to 7.4Ak, shows in the latter a much greater shape diversity, both in toe and metatarsal impressions. Such diversity could not be readily explained by differences in leg/foot stance, penetration in the sediment substratum, and retraction, which is the mechanism that explains shape differences in the experimental study. Because of this, Alternative 3, although possible, seems less likely an explanation than Alternative 2.

Ichnological Assessment: Introductory Remarks
The features displayed by MVs Aa to Ad are reminiscent of those of small theropods, as characterized by Lull (1953), Thulborn and Wade (1984), Thulborn (1990), and others, who set forth the following characters as diagnostic of small theropod footprints: (a) shape oval, sub-elongated to elongated, so that the width is 70% to 75% of the antero-posterior length; (b) general small size, with an antero-posterior length usually

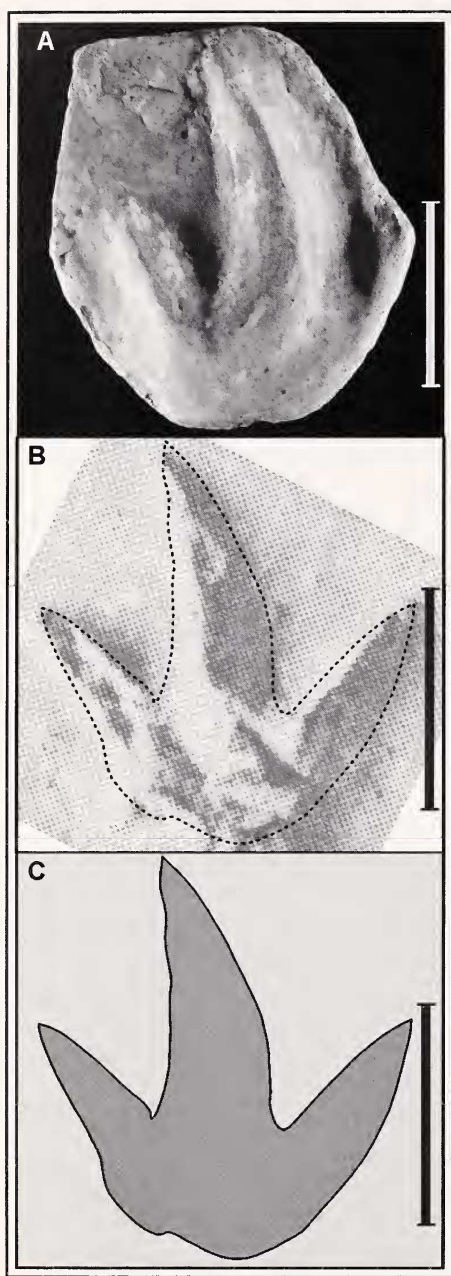


Figure 9A–C Ichnological comparison of Morphotype A with *Shensipus*. Prints are adjusted to the same size to ease comparisons. Scale bar = 5 cm. 9A, IGM-7428, an epirelief cast of a left pedal print assigned to MV Aa; 9B, *Shensipus tungchuanensis* Young (1960) from the Middle Jurassic of China, virtual left print, (after Zhen et al., 1989:fig. 19.4E; point line added to better delineate the ichnite); 9C, outline of print depicted in 9B to enhance the shape

(between digits II and IV) usually does not exceed 50° ; (e) step angle between 150° and 180° , which indicates a small pedal divergence angle, and that the gait was that of narrow-hipped individuals. The estimated hip height (~ 0.6 m) is that of small individuals.

The hyperelongated, human footprint-like appearance of MVs Ae to Af, admittedly uncommon, has already been documented in theropods from several sites across the world: North America, Early Jurassic: (Connecticut Valley (Lull, 1953)), Cretaceous: (Utah (Strevell, 1940), Texas (Kuban, 1989; Pittman, 1989)); China, Late Jurassic: (Sichuan Province (Zhen et al., 1989)); Europe, Cretaceous: (Spain (Brancas et al., 1979)); North Africa, Middle Jurassic: (Morocco (Ambroggi and Lapparent, 1954)); Australia, Cretaceous: (Queensland (Thulborn and Wade, 1984)); South America, Late Jurassic/Early Cretaceous: (Brazil, Paraiba (Leonardi, 1994)). Kuban (1986, 1989) reviewed possible explanations, and concluded that most frequently, this elongated footprint shape involves a metatarsal impression, made while the theropod track maker adopted a plantigrade or semiplantigrade gait. The description and discussion of MVs Aa to Ak as integrating a morphic spectrum strongly support Kuban's conclusion. Morphotype A footprints then are thus interpreted as those of small theropods.

Ichnogeneric Summary Review

Formally described Jurassic (and/or Late Triassic) ichnogenera attributed to small theropods (i.e., 'coelurosaurs' in a precladistic sense) are rather numerous and geographically quite widespread; among the better known are *Anchisauripus* Lull 1904, *Atreipus* Olsen and Baird 1986, *Coelurosaurichnus* Huene 1941, *Delatorreichnus* Casamiquela 1964, *Grallator* Hitchcock 1858, *Laiyangpus* Young 1960, *Otouphepus* Cushman 1904, *Paracoelurosaurichnus* Zhen, Zhen, and Rao 1986, *Sarmientichnus* Casamiquela 1964, *Schizograllator* Zhen, Zhen, and Rao, *Seleichnus* Hitchcock 1858, *Shensipus* Young 1966, *Stenonyx* Lull 1953, *Taupezia* Delair 1962, and *Wild-eichnus* Casamiquela 1964.

It should be noted that the detailed stratigraphic study of the Newark supergroup of New England conducted by Olsen (1980) and Olsen and Baird (1986), has led to the geochronologic reassignment to the Early Jurassic of several ichnogenera such as *Anchisauripus*, *Grallator*, *Otouphepus*, *Seleichnus*, and *Stenonyx*, originally described from the Connecticut Valley by Lull, (1953) and assigned by him to the Late Triassic. We go along with this change, but keep open to the possibility that some such ichnogenera might be also of Late Triassic age. With this in mind, we proceed to compare Morphotype A with the ichnogenera mentioned in the preceding paragraph.

Anchisauripus (Late Triassic and possibly Early Jurassic of eastern North America (Lull, 1953;

no greater than 20 cm; (c) mesaxononic tridactyl, with clawed digits directed anteriorly; (d) digits II and IV shorter, subequal, relatively broader than digit III, which is the longest, diverging nearly symmetrically from it; the total divergence angle

Olsen, 1980; Olsen and Baird, 1986), Early Jurassic of Brazil (Leonardi, 1994)) resembles and co-occurs with *Grallator* in eastern North America; because of this some people regard it as a synonym of the latter. The taxonomic review of this problem lies beyond the scope of this paper; here, for the sake of completeness, we regard both as independent ichnogenera. Morphotype A tracks are ~20% to 30% antero-posteriorly shorter, but much wider (~60% and more) than those of *Anchisauripus*; have less robust, subequal toes with poorly developed pads; and a much greater divergence angle. In contrast, *Anchisauripus* shows rather narrow tracks with robust, unequal toes (digit III is much longer than II and IV); well-developed pads; and a small divergence angle (~48°).

Morphotype A tracks fall in the size range of those of *Atreipus* (Late Triassic and probably Early Jurassic of eastern North America (Olsen and Baird, 1986); and Late Triassic of Europe (Germany: Olsen and Baird, 1986)). According to Olsen and Baird (1986), *Atreipus* includes *Anchisauripus*, *Coelurosaurichnus*, and some species of *Grallator*; they are probably right, but this is no place to attempt a formal revision of these taxa, so for the sake of completeness, we treat them as independent ichnogenera. Morphotype A tracks differ from those of *Atreipus*, being wider and relatively shorter (length:width ratio = 1.0:0.65 to 1.0:0.90, vs. 1.0:0.50 to 1.0:0.57 in *Atreipus*), have a poorly developed plantar region, and moderately robust, subequal toes, which display a large divergence angle (frequently ~60°, whereas in *Atreipus* divergence angle is commonly 28° to 32°).

Morphotype A tracks are ~15% to 35% longer and two times wider than those of *Coelurosaurichnus* (Middle Jurassic of France (Kuhn, 1958; Demathieu, 1989)), and also differ from them in having less robust, subequal toes; in *Coelurosaurichnus* digit III is much longer than the others. Morphotype A tracks are ~40% to 50% smaller than those of *Delatorreichnus* (Late Jurassic of Argentina (Casamiquela, 1964)), and differ also from them in having less robust toes and a shorter plantar region.

Morphotype A tracks fall in the size range of *Grallator* (Late Triassic and probably Early Jurassic of eastern North America (Lull, 1953; Olsen, 1980; Olsen and Baird, 1986), Early Jurassic of China (Young, 1960; Zhen et al., 1986); Early Cretaceous of Brazil (Leonardi, 1994); *Grallator* includes *Dilophosaurus* (Early Jurassic of South Africa (Ellenberger, 1972) and possibly of Arizona (Irby, 1996)). Morphotype A differs from them in having subequal, rather robust toes, which display a large divergence angle; by contrast, in *Grallator* digit III is much longer than II and IV, pads are well developed, and the divergence angle is small (~45°), thus having the configuration of a narrow track (i.e., much longer than wide).

Morphotype A tracks are at least five times larger than those of *Laiyangpus* (Late Jurassic of

China (Young, 1960)), which in addition show delicate, subparallel, acuminate digits, thus being quite different from those of Morphotype A. Morphotype A tracks fall in the size range of those of *Otouphepus* (Late Triassic and probably Early Jurassic of eastern North America (Lull, 1953; Olsen and Baird, 1986)), but are proportionally wider and have less robust, subequal toes, which display a large divergence angle. In contrast, *Otouphepus* tracks have very robust toes, particularly so digit III, which is much longer than the other digits; the divergence angle is small (~35°), thus shaping a narrow track. Morphotype A tracks are nearly half as large as those of *Paracoelurosaurichnus* (Early Jurassic of China (Zhen et al., 1986)), which show narrow, delicate digits, small divergence angle (~45°), and digit III much longer than II and IV; hence these tracks are very different from those of Morphotype A.

Morphotype A tracks are slightly longer, but two to three times wider than the only known footprint of *Sarmientichnus* (Middle Jurassic of Argentina (Casamiquela, 1964)), which shows only one well-developed toe print (digit II?), and thus its maker was interpreted by Casamiquela as functionally didactylous; hence *Sarmientichnus* is very different from this morphotype.

Morphotype A tracks are at least half as large as those of *Schizograllator* (Early Jurassic of China (Zhen et al., 1986)), which show moderately robust, unequal toes (digit III is much longer than II and IV), with well-developed pads, thus contrasting in shape with Morphotype A tracks, whose toes are subequal. Morphotype A tracks are ~27% to 38% longer and three to four times wider than those of *Seleneichnus* (Late Triassic and probably Early Jurassic of eastern North America (Lull, 1953; Olsen and Baird, 1986)), which show an odd ellipsoidal shape, largely made by the plantar region, with three very unequal toe impressions on the anterior margin (that of digit III is by far the longest). The track maker is interpreted as functionally didactylous (Lull, 1953). In contrast, Morphotype A tracks are tridactylar, with poorly developed plantar region, and moderately robust, subequal toes. Morphotype A tracks are ~25% larger than those of *Shensipus* (Middle Jurassic of China (Young, 1966; Haubold, 1971, 1984; Zhen et al., 1983, 1989)), but show a close overall resemblance, particularly so with MV Aa2 (Figures 8.1 and 9); both have subequal, distally tapering, slightly curved toes, seemingly devoid of pads, and a poorly developed plantar region; their divergence angle is similar. Yet, we have decided to regard Morphotype A and *Shensipus* as different, but related, ichnotaxa, on the basis of the size difference, the scant material basis (which precludes assessing intraspecific variation), and the enormous geographic separation between southeastern Mexico and China.

Morphotype A tracks are ~3.6 to 4.3 times larger than those of *Stenonyx* (Late Triassic and

probably Early Jurassic of eastern North America (Lull, 1953; Olsen and Baird, 1986)), which have a very small plantar region and short, robust unequal toes (digit III is much longer than II and IV) with well-developed pads. Morphotype A tracks have a better developed plantar region, and subequal toes. Morphotype A tracks are ~15% to 25% smaller than those of *Taupezia* (Middle Jurassic of England (Delair, 1962)), and have very different morphological features. *Taupezia* tracks are quite reminiscent of those experimentally generated by extant birds walking on very wet sediments (Gatesy et al., 1999); such prints are similar to those of Late Triassic small theropods from eastern Greenland. So, all that can be said about *Taupezia* tracks is that their maker was a small theropod.

Morphotype A tracks are ~34% to 44% larger than those of *Wildeichnus* (Middle Jurassic of Argentina (Casamiquela, 1964)), which show a moderate to well-developed plantar region, and very unequal, delicate (i.e., narrow and long) toes, so that digit III is much longer than II and IV. These tracks then are very different from those of Morphotype A, which have a poorly developed plantar region, and moderately robust, subequal toes. Summing up then, it could be said that although Morphotype A tracks show some resemblance to the Middle Jurassic ichnogenus *Shensipus* (from China), the scant material basis, size differences, and great geographic separation make it inadvisable to formally refer Morphotype A to this ichnogenus.

Possible Correspondence with Linnean Taxonomic Categories

By middle Early Jurassic time, *Syntarsus* (Late Triassic of South Africa (Raath, 1969); Kayenta Fm., Arizona, (Rowe, 1989; Glut, 1997) was the only known survivor of the coelophysoid ceratosaurs (*sensu* Holtz, 1994, and Tikosky and Rowe, 2004), which represent the first extensive theropod radiation (Rowe and Gauthier, 1990; Rowe et al., 1997; Tikosky and Rowe, 2004). *Syntarsus* was a small to medium-size, gracile, digitigrade coelophysoid; its feet (described and figured by Raath, 1969, and Glut, 1997:873) were functionally tridactylar, with a dactylar length ~120 mm, which falls in the length range of Morphotype A, but with a width of ~60 mm, thus 20% to 45% narrower than the latter, and would have produced narrow tracks with a small divergence angle, quite unlike that of Morphotype A. Subsequent ceratosaurs (Neoceratosauria Novas 1991, *sensu* Tikosky and Rowe, 2004) are Late Jurassic to Late Cretaceous theropods of medium to large size (cf. Gilmore, 1920), hence much larger than the morphotype trackmaker.

The Tetanurae (*sensu* Gauthier, 1986) constitute the second major radiation of theropod dinosaurs, ranging from the Middle Jurassic to the Late Cretaceous; basal tetanurans (*sensu* Holz et al.,

2004) of Middle Jurassic age include megalosaurids, chiefly from Europe (Glut, 1997, 2000, 2002, 2003; Holz et al., 2004), all medium-size to large theropods; the small *Proceratosaurus* from England (Huene, 1926); a coelurosaur (*sensu* Holz et al., 2004) of uncertain position, whose feet are unknown, so no comparison is possible with Morphotype A; and several genera of uncertain position (cf. Holtz et al., 2004:table 4.1), mostly of medium to large size, whose foot morphology is unknown or undescribed. Coelurosaurs extensively diversified in the Late Jurassic-Cretaceous, developing small, medium, and mostly large-size theropods. The Morphotype A trackmaker is roughly the size of the North American Late Jurassic *Ornitholestes* (cf. Osborn, 1903:fig. 1; Ostrom, 1978, 1980), differing from it in having rather thick digits (cf. Figures 8.1.Aa, 8.1.Ab, and 8.2.Ac) and in being geologically older. *Coelurus*, coeval and sympatric with *Ornitholestes*, is of similar size (cf. Marsh, 1884; Ostrom, 1980:fig. 2; Miles et al., 1998), but its precise foot structure remains undescribed. These reasons preclude assigning the Morphotype A trackmaker to either *Coelurus* or *Ornitholestes*.

Summing up, because of their greater recorded Middle Jurassic diversity and pedal morphology, it seems probable that the Morphotype A trackmaker represents a taxon that could have belonged to basal coelurosaurs (*sensu* Holz et al., 2004).

Geographic Distribution and Geological Age

Bajocian–Early Bathonian ‘coelurosaur’ (~ small theropod) footprints are known from South America (Brazil and Argentina (Casamiquela, 1964; Leonardi, 1989, 1994)); Australia (Weishampel, 1990); Europe (southeastern England (Delair, 1962; Lockley and Meyer, 2000) France (Kuhn, 1958; Demathieu, 1989)); China (Young, 1966; Haubold, 1971, 1984; Zhen et al., 1983; 1989); and western North America (Carmel Formation, eastern Utah (Lockley et al., 1998; Hamblin et al., 2000) Lower Sundance Formation, Wyoming (Breithaupt et al., 2003) and Oaxaca, southeastern Mexico (this study)). The footprints from Oaxaca extend the record ~3,000 km southward, making it the southernmost Middle Jurassic sample for the Northern Hemisphere.

Suborder Theropoda Marsh, 1881

Tetanurae Gauthier, 1986

Avetheropoda Paul, 1988

Carnosauria (Huene, 1914),
sensu Holtz et al., 2004

Allurosauroidea Currie et Zhao, 1993,
sensu Holtz et al., 2004

Allosauridae Marsh, 1879

?Allosauridae

Morphotype B

(Figure 10, Table 4)

DESCRIPTION. Large subrounded tridactyl pedal print, digits II and IV short and thick, less

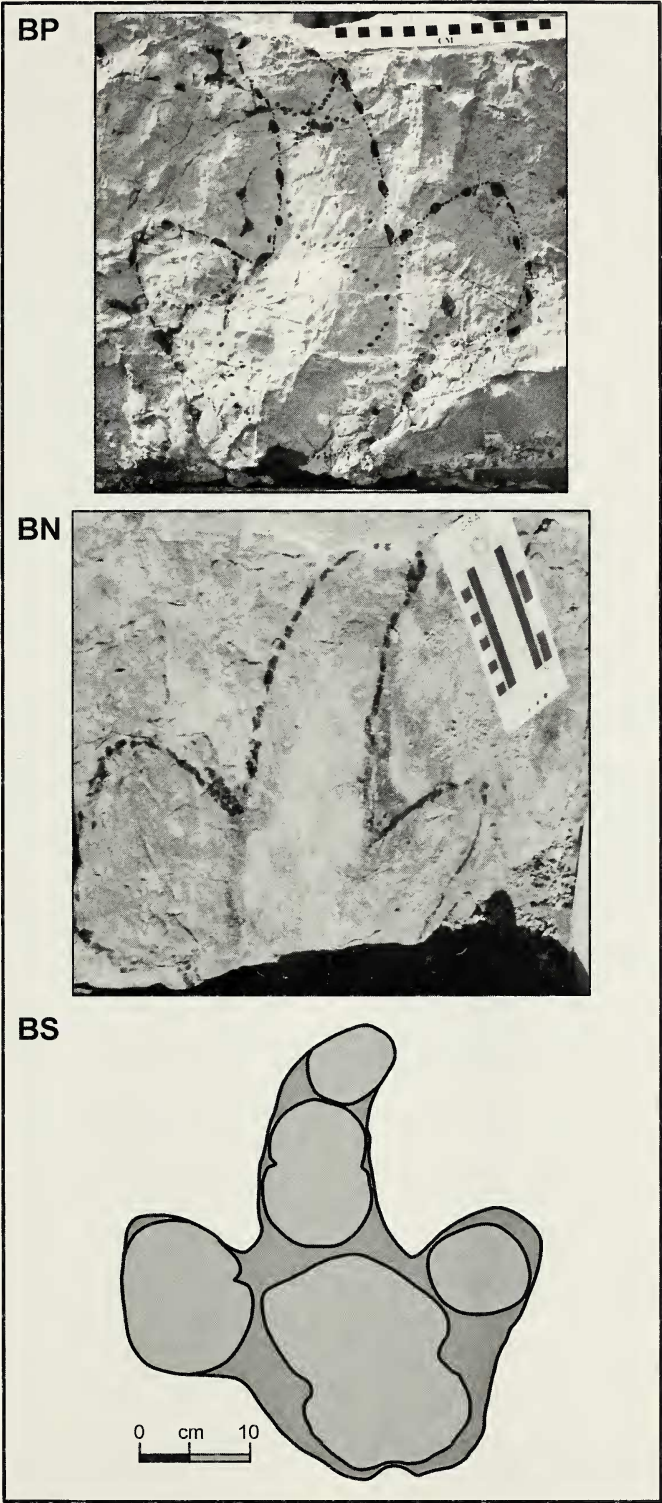


Figure 10 Morphotype B, single footprint originated by a track maker referred to ?Allosauridae; BN, outcrop photograph of a large left footprint; outlined to enhance visibility; BP, photograph of IGM-7959, epirelief cast of this footprint; BS, a computer drawing of the same footprint from a blow up of the photograph, and of IGM-3006, plastic sheet silhouette record of the footprint outlined in the outcrop, scale bar = 10 cm

Table 4 Measurements of the left footprint assigned to Morphotype B ABBREVIATIONS as in Table 2. (A), morphometric ratio method: $h = 4.9 \text{ fl}$ (Thulborn, 1990:251, Equation 8.3); (B), allometric equation method: $h = 3.14 \text{ fl}^{1.14}$ (Thulborn, 1990:254, Equation 8.11); (C), allometric equation method: $h = 8.6 \text{ fl}^{0.85}$ (Thulborn, 1990:254, Equation 8.10). Linear measurements in mm

Measurements	Data
Fl	391
fw	340
H (A)	1916
H (B)	1397
H (C)	2855
dIII	72
dwII	96
dl III	180
dwIII	116
dlIV	60
dwIV	100
DA	70°
aiII-III	30°
aiIII-IV	40°

than half the length of digit III, which is curved inward; a well-developed lateral notch reaches inside the interdigital notch between digits III and IV, so that the digit IV stands out from the rest of the print. The pads are barely discernible: there is one in digits II and IV, and two in digit III; the plantar pad seems to be four-lobed; no traces of the claws are distinguishable. The total divergence angle is 70°; the estimated hip height is ~1.91 m. It should be noted that digit III shows a marked curvature that makes its tip diverge 30° from the antero-posterior digit axis; such curvature is much greater than in other large theropod footprints (cf. Lockley and Meyer, 2000:146, fig. 6.11). Whether this curvature resulted from preservational distortion, an anatomical anomaly, or a normal structure can not be resolved at present.

REFERRED MATERIAL. IGM-7959, epirelief plaster cast of a single left footprint located in the smaller outcrop, 1 m from its eastern margin (Figure 10BP); IGM-3006, plastic sheet with the silhouette of this footprint directly outlined in the outcrop (Figures 10BN and 10BS).

GENERAL DISCUSSION OF THE MORPHOTYPE

Ichnological Assessment: Introductory Remarks
The footprint closely resembles that of typical theropods in having a significantly longer digit III, and a deep lateral notch that makes digit IV fully stand out from the rest of the foot (Lull, 1953; Thulborn, 1990); its size fits that of large theropods, that is, carnosaurs (cf. Haubold, 1971, 1984; Lockley and Hunt, 1995; Lockley and Meyer, 2000).

Ichnogeneric Summary Review
Named Early and Middle Jurassic large theropod ichnogenera are few and far apart; among the better known are *Changpeipus* Young, 1960, *Dilophosauripus* Ellenberger, 1970, *Eubrontes* Hitchcock, 1845, *Kayentapus* Welles, 1971, *Megalosauripus* Lockley, Meyer, and dos Santos, 1996, and *Youngichnus* Zhen, Zhen, and Rao, 1986. Given that the formal nomenclatorial and taxonomic status of some mentioned ichnogenera is not settled, before comparing Morphotype B to them, some comments are in order. Olsen (1980) and Pittman (1992) have discarded ichnotaxa based on insufficient material and/or unsatisfactory descriptions, and have synonymized ichnotaxa that share the character states already recognized in another ichnotaxon, for instance *Grallator* includes as junior synonyms *Eubrontes*, *Changpeipus*, *Kayentapus*, *Megalosauripus*, and *Youngichnus*.

Lockley and Hunt (1995) recognized merit in Olsen's and Pittman's approach, but regard *Eubrontes* as a valid genus diagnostically different from *Grallator*; further, they synonymized *Kayentapus* to *Eubrontes* and *Dilophosauripus* to *Grallator*, and cited them as examples of 'provincial taxonomy', that is, assigning new names to tracks from a localized area, where suitable names already exist. Lockley and Hunt were aware of the problematic status of *Megalosauripus*, but chose to regard it as a valid ichnogenus, and used it as the basis of intercontinental correlation (Lockley and Hunt, 1995). We concur with the ideas expressed above, but for the sake of completeness, we shall compare Morphotype B with the ichnogenera mentioned, except *Dilophosauripus* and *Kayentapus*, following Lockley and Hunt (1995).

The Morphotype B track is ~10% to 25% larger than those of *Changpeipus* (Early and Middle Jurassic of China (Young, 1960)), and differs from them in having shorter, stouter toes; a wider plantar (~metatarsal) region; and a much greater divergence angle (70° vs. 45° in *Changpeipus*). The Morphotype B track is ~15% to 45% larger than those of *Eubrontes* (Late Triassic and probably Early Jurassic of eastern North America (Lull, 1953; Olsen, 1980; Olsen and Baird, 1986), southern United States (Lockley and Hunt, 1995); it includes *Kayentapus* southern United States (Welles, 1971; Lockley et al., 1995)), and also differs from them in having shorter and stouter toes, with larger and less numerous pads, and a larger plantar region; the divergence angle is larger than that of most *Eubrontes* tracks, but some *Eubrontes* tracks show a divergence angle as large or larger than that of Morphotype B. It appears that the maker of the Morphotype B track was somewhat heavier and/or more plantigrade than the maker of *Eubrontes* tracks.

The Morphotype B track is ~10% longer but 18% wider than the tracks of *Gigandipus* Hitch-

cock, 1855 (Late Triassic and probably Early Jurassic of eastern North America (Lull, 1953; Haubold, 1971, 1986; Olsen and Baird, 1986). Olsen and Baird (1986:64) regard *Gigandipus* (?*Anchisauripus*) *milfordensis* as the type species of their new ichnogenus *Atreipus*, but do not state whether *Gigandipus* remains valid or invalid; other authors (cf. Haubold, 1971, 1986) deem it valid, and here we follow their opinion. The Morphotype B track also differs from *Gigandipus* tracks in having shorter toes, longer and curved digit III, greater divergence angle (70° vs. 50° in *Gigandipus*), and the lack of hallux. The Morphotype B track is much larger (3.5 times longer and five times wider) than tracks of *Hyphepus* Hitchcock 1858 (Late Triassic of eastern North America (Lull, 1953)) and further differs from them in having longer and stouter toes, curved digit III, shorter plantar region, and a greater divergence angle (70° vs. 45° in *Hyphepus*).

The Morphotype B track is ~13% to 48% smaller than those of *Megalosauripus* (*sensu* Lockley et al., 1986, 1996b; Middle Jurassic of western United States (Lockley et al., 1996b), England (Lockley and Meyer, 2000); Late Jurassic of Europe (Nopcsa, 1923; Haubold, 1971), western Asia (Lockley et al., 1996b); Early Cretaceous of Australia (Colbert and Merrilees, 1967), and Uzbekistan (Gabuniya and Khurbatov, 1988)), and differs from them in having shorter, stouter toes with a greater divergence angle (70° vs. 55° to 60° in *Megalosauripus*), more curved digit III, larger and less numerous pads, and a larger plantar region. The Morphotype B track is ~30% longer and ~45% wider than those of *Youngichnus* (Early Jurassic of China, Zhen et al., 1986), and differs from them in having shorter and stouter toes, a greater divergence angle (70° vs. 40° in *Youngichnus*), more curved digit III, narrower plantar region, and better developed pads. Summing up, Morphotype B is diagnostically different from the ichnogenes discussed above; in fact this morphotype could be the basis of a new ichnogenus; however we refrain from formally proposing it, because of the scarce available material.

Possible Correspondence with Linnean Taxonomic Categories

Large Middle Jurassic theropods are represented by the Megalosauridae Huxley 1869, *sensu* Holtz et al., 2004 (chiefly from western Europe (Holtz et al., 2004:table 1), the Carnosauria Huene 1920, *sensu* Holtz et al., 2004 (from China (Dong, 1992; Zhao and Currie, 1993), and Antarctica (Hammer and Hickerson, 1994), unfortunately no published description of their feet is available) and a few tetanurans of uncertain position (cf. Holtz et al., 2004:table 4.1). In spite of its complex taxonomic/nomenclatorial history (Glut, 1997), *Megalosaurus* Huxley, 1869 is the best known megalosaurid (Padian, 1997): it

reached 7 to 8 m long; it was tridactylous and fully digitigrade, with feet long and narrow; footprints attributed to it are 640 mm long and 210 mm wide (Lapparent and Zbyszewski, 1957). A similar foot structure is seen in other megalosaurids (e.g. *Piatnizkysaurus* Bonaparte, 1979). In contrast, Morphotype B is much wider, and its track maker would have had a foot structure closer to that of allosauroids *sensu* Currie and Zhao, 1993, for example the eponymous *Allosaurus*, who had robust hind limbs with digits II–IV evenly spaced (Glut, 1997:107). Although allosauroids are known from the Late Jurassic of North America and the Cretaceous of South America, North Africa, and North America (Holz et al., 2004), and megalosaurids were fairly common in the Middle Jurassic (Padian, 1997), we deem it more probable that the track maker of Morphotype B, because of its closer inferred foot structure, may have been an early member of the Allosauroidea (*sensu* Holtz et al., 2004), not yet represented by bone remains. Support for this hypothesis stems from the discovery of sauropod bone remains (Buffeteau et al., 2000) from an earlier age than previously known (cf. McIntosh, 1990; Glut, 1997), but suspected on the basis of ichnological evidence (Lockley et al., 2001).

Geologic Age and Geographic Distribution

Large Jurassic theropod tracks, although not numerous are known nearly worldwide: North America, Late Triassic and possibly Early Jurassic: New England region (Lull, 1953; Haubold, 1971, 1986; Olsen, 1980; Olsen and Baird, 1986); Early Jurassic: Arizona (Kayenta Formation, Navajo Sandstone (Welles, 1971; Thulborn, 1990)), Utah (Moenave Formation (Miller et al., 1989)); Middle Jurassic: Colorado and Utah (Summerville Formation and Entrada Sandstone of the Moab Megatracksite (Lockley, 1991a; Lockley and Hunt, 1995; Lockley et al., 1996a)); Late Jurassic: Mexico and Colorado (Playa Azul, Michoacán, Mexico (Ferrusquía et al., 1978), Morrison Formation (Lockley et al., 1986)). Europe, Middle Jurassic: United Kingdom (Oxfordshire, southern England (Lockley and Meyer, 2000), Hebrides Isles of Scotland (Andrews and Hudson, 1984)), Portugal (near Fátima (Dos Santos et al., 1994)); France and Germany, Middle and Late Triassic (Nopcsa, 1923; Haubold, 1971); China, Middle Jurassic: Sichuan (probably Xiashaximiao Formation (Young, 1960)); western Asia: Late Jurassic, Turkmenistan/Uzbekistan region (Lockley et al., 1996b); and South America: Brazil, Late Triassic or Early Jurassic: Paraná Basin, southern Brazil (Botucatu Formation (Leonardi, 1994)); Middle or Late Jurassic: Chile (Tarapaca Province (Galli and Dingman, 1965)). The Xochitlapilco find in southeastern Mexico adds a sixth site to the meager record of Middle Jurassic large theropod footprints worldwide.

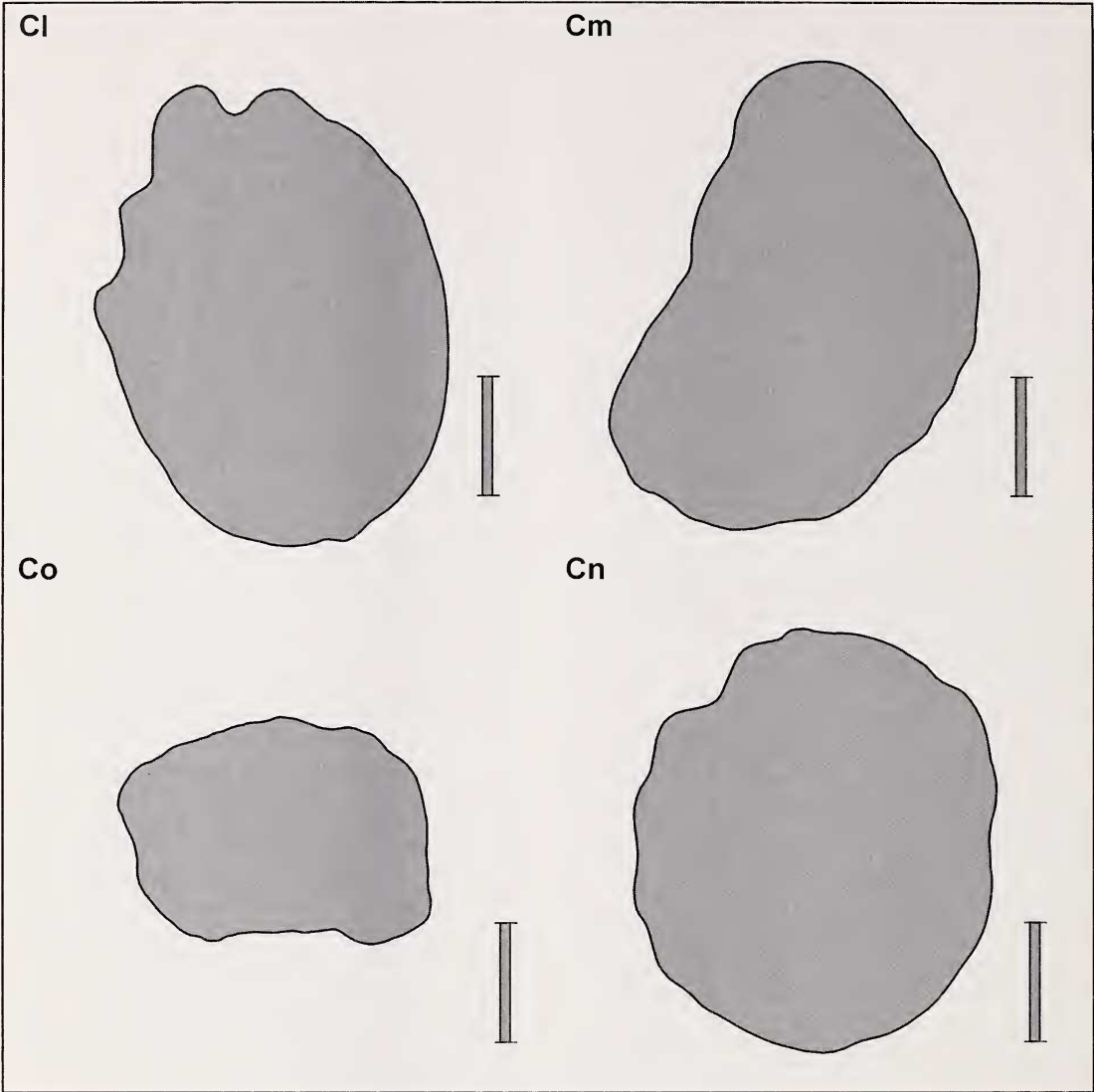


Figure 11 Morphotype C, footprint assemblage originated by track makers referred to an undescribed family of Eusauropoda Upchurch, 1995; scale bar = 5 cm; Cl (f# 26, left), Cm (f# 8, right), and Cn (f# 19, left), pedal prints; Co (f# 28, left), manual print; all are computer drawings of selected tracks silhouettes from IGM-7958, plastic sheet outline record of tracks exposed on the main outcrop, assigned to MVs Cl, Cm, Cn, and Co respectively. (f# = footprint number)

Suborder Sauropodomorpha Huene, 1932
Infraorder Sauropoda Marsh, 1878
Eusauropoda Upchurch, 1995
Family Undescribed
Morphotype C, Morphic Varieties Cl–Co
(Figure 11, Table 5)

DESCRIPTION. Small, oval to subrounded pedal prints (most fall in the 16- to 19-cm antero-posterior length range), with a wide planar region, and short, antero-laterally directed digits. The only manual print is antero-posteriorly much shorter than the pedal prints; its outline is such that the dorsal ('external') margin is convex,

whereas the palmar margin is concave; one of the side margins is concave too, and the opposite is nearly straight. The estimated hip height ranges between 56 and 116 cm; other measures and numerical parameters are given in Table 5.

Morphic Variety Cl

REFERRED MATERIAL. IGM-7958, plastic sheet, pedal impressions numbers 20, 26 (left, Figure 11Cl), and 27 (indeterminate).

DESCRIPTION. The footprints of this morphic variety are the most clearly sauropodal ones, and from them the morphotype characterization was made. It should be noted though, that in the

Table 5 Measurements (in mm) of pedal and manual prints assigned to Morphotype C ABBREVIATIONS as in Table 2. (A), morphometric ratio method: h = 5.9 fl (Thulborn, 1989:42); (B), morphometric ratio method: h = 4.0 fl (Alexander, 1976:129)

F#	Side	MV	fl	Fw	H (A)	H (B)
20	L	Cl	189	145	1115	756
26	L	Cl	197	153	1162	788
27	I	Cl	160	187	944	640
7	R?	Cm	166	133	979	664
8	R	Cm	221	106	1304	884
11	L?	Cm	176	112	1038	704
17	L?	Cn	160	90	944	640
18	I	Cn	129	98	761	516
19	L	Cn	182	146	1073	728
21	R?	Cn	180	143	1062	720
30	L?	Cn	172	138	1014	688
32	L?	Cn	140	120	826	560
33	I	Cn	140e	110	826	560
28	L	Co	91	123	—	—

footprint 26, where the dactylar impressions are best preserved, digit I has a rounded tip, whereas digits III and IV have slightly acute tips; digit II shows a small prominence that might be a claw mark; digit V is not preserved.

DISCUSSION. The sauropod pes was graviportal, with reduced digits protected at the tip by ungual claws of diminishing size from digit I to III (McIntosh, 1990); this basic anatomical structure is reflected in the footprints. The MV Cl footprint differs from the typical sauropod one in having the clawlike mark only in digit II; whether it corresponded to an anatomical structure or it is an artifact can not be ascertained because of the limited available sample.

Morphic Variety Cm

REFERRED MATERIAL. IGM-7958, plastic sheet pedal impression numbers 7, 8 (right, Figure 11Cm), and 11 (?left).

DESCRIPTION. The footprints of this variety are oval, slightly longer than those of MV Cl, and show minor lobes on the lateral margin that might correspond to toe marks.

DISCUSSION. The antero-posterior elongation of this morphic variety is an uncommon feature for sauropod footprints. Rather than representing a structural peculiarity, such elongation might be the result of asymmetrical printing between the external and internal halves of the print, whereby the half receiving relatively greater pressure would be more deeply imprinted than the other; in underprints the better defined half would usually be wider than the other, thus producing a virtual elongation that is not present in the true footprint. Larger sauropod footprints with this general shape have already been reported in the literature (cf. Pittman and Gillette, 1989).

Morphic Variety Cn

REFERRED MATERIAL. IGM-7958, plastic sheet, pedal impression numbers 17, 19, 30, and

32 (?left), 21 (?right), 18 and 33 (indeterminate), Figure 11Cn.

DESCRIPTION. Half of the sauropod footprints belong to this morphic variety, it is the least typical for the lack of toe impressions, so that the plantar region remains.

DISCUSSION. Poorly preserved, ovoid to subrounded footprints with no digit marks have already been reported in the literature, and interpreted as being made by sauropods (cf. Thulborn, 1990).

Morphic Variety Co

REFERRED MATERIAL. IGM-7958, plastic sheet, number 28 corresponds to a manual impression, Figure 11Co.

DESCRIPTION. Only one of the 15 sauropod footprints is referred to this morphic variety. Because it was described in the characterization of Morphotype C, there is no need to repeat its description here.

DISCUSSION. The manual print is located very close to footprint 27 (MV Cn); both prints have their greatest axes parallel, however such axis is transverse to the antero-posterior axis in the manus print, whereas it largely corresponds to the antero-posterior axis in the podial prints. This spatial relationship suggests that the track maker of footprint 27 also produced the manual print 28. If so, the manus contacted the ground in a position that was not outwardly rotated relative to the sagittal plane of the individual (in a ground sloth fashion), which is unlike the transverse or oblique manus ground contact, usual among sauropods (Farlow et al., 1989; Thulborn, 1989; Pittman, 1992).

The pedal:manual print ratio recorded in the Xochitlapilco assemblage (14:1) is far from the expected 1:1 ratio of sauropods. Several possible explanations include the following:

1. Differential preservation favoring pedal over manual prints might be the cause; however, the

print-bearing strata show no compositional or sedimentary-structural differences that could support such an interpretation.

2a. The track maker had a specialized body structure and/or gait that placed less weight to the fore limbs than to the hind limbs, hence the manual prints would have been less deep, and would have had a lesser chance of preservation. The small number of prints and the lack of skeletal remains make it impossible to test this hypothesis, which in any case is contrary to the tendency for manus to be overrepresented in many samples (Lockley et al., 1994).

2b. The footprints are actually underprints made as in (2a). The shallowness of the prints argues in favor of this hypothesis, but it is still open to the same objections as (2a).

3. The footprints were made subaqueously, that is, by sauropods walking/paddling over ground covered by shallow water. The lack of striations or drag marks on the prints is inconsistent with this hypothesis (cf. McAllister, 1989).

4. Overprinting obliterated the manual prints (cf. Lockley, 1991b:216; Paul, 1991). Overprinting commonly occurs in graviportal tetrapods where the length of the hind and fore limbs is similar, the distance between them is close or equal to such length, and the pes is larger than the manus; thus the hind and fore limbs may partly or fully overlap resulting in erasure of the front footprints. The lack of appendicular skeletal material and/or trackways does not allow one to test this hypothesis. Full overprinting is not common (see Farlow et al., 1989, and Lockley et al., 1986, for well documented instances and further observations), so that most trackways show both front and hind footprints nearly equally represented (cf. Lockley and Hunt, 1995; Lockley and Meyer, 2000).

5. The track maker was a facultative biped. Again, the lack of skeletal material and/or trackways make it impossible to test this hypothesis. Alexander (1985) and Bakker (1993) have proposed that some sauropods were able to adopt a tripod-based standing/sitting position, supporting their weight on the hind limbs and the tail. The lack of tail impressions in the Xochixtlapilco assemblage argues against this explanation.

Summing up, the available evidence allows no positive choice from the possible explanations discussed; however, it seems probable that the observed manual:podial print ratio in the Xochixtlapilco assemblage represents some sort of a preservational artifact.

GENERAL DISCUSSION OF THE MORPHOTYPE

Morphotype Assignment

The sauropod footprints referred to this morphotype are similar in shape, size (most fall in the 16- to 19-cm antero-posterior length range), and

parameters (both configurational and numerical, Table 5); these facts indicate that quite probably, the track makers belonged to the same population.

Ichnological Assessment: Introductory Remarks

The limited number, moderate to poor preservation, and small size of the Morphotype C prints render difficult the identification of the track maker. Thulborn (1990) has diagnosed the sauropod footprints as (a) ovoidal to subround, wider than long; (b) usually large (antero-posterior length range: 20 cm to 100 cm, commonly 30 to 60 cm), however, undoubtedly small sauropod footprints have been reported, such as those of the Jindong Formation, from the Cretaceous of Korea (Lim et al., 1989, 1994); (c) pentadactyl, with digits oriented antero-laterally, (MV Cl shows at least three digits so oriented); (d) having a well-developed plantar pad (the shallowness of the Xochixtlapilco prints suggests that they are either underprints where the pad impression is not preserved, or that most of the footprint thickness has been eroded); and (e) having a step angle of 120°–140° (the lack of trackways does not allow us to detect this character). Sauropod manual prints are (f) about half as large as the corresponding pedal prints, (g) transversely much wider than antero-posterior long, (h) semicircular to horseshoe-shaped, (i) lacking digital marks, (j) convex at the anterior margin and concave at the palmar one. As shown, the Morphotype C prints have most of these features, which allows one to refer the track maker to the Sauropoda.

Ichnogeneric Summary Review

There are few named sauropod ichnogenera, and most belong to the Cretaceous; for example, *Breviparopus* Dutuit and Ouazzou, 1980 (Early Cretaceous of the Gulf Coast (Farlow et al., 1989; Pittman, 1992)), *Rotundichnus* Hendricks, 1981 (Early Cretaceous of Germany (Hendricks, 1981)), and *Koreanosauripus* Kim, 1986 (Late Cretaceous of Korea (Kim, 1986)); among the named Jurassic ichnogenera are *Breviparopus* (Late Jurassic of Morocco (Dutuit and Ouazzou, 1980)) and *Gigantosauropus* Mensink and Mertmann, 1984 (Late Jurassic of Spain (Mensink and Mertmann, 1984)); all are much larger than Morphotype C, and need no further consideration.

Three small named ichnogenera attributed to sauropods merit discussion: *Agrestipus* (Late Triassic of Virginia, eastern United States (Weems, 1987)), *Tetrasauropus* Ellenberger, 1970 (Late Triassic of western United States (Lockley et al., 2001)), and *Hamanosauripus* Kim, 1986 (Late Cretaceous of Korea (Kim, 1986)). Morphotype C differs from *Agrestipus* Weems, 1987 in having ovoid rather than trapezoidal, posteriorly narrower pedal prints, with well-discernible toes located on the antero-lateral margin (in *Agrestipus* no toes are discernible, instead very faint promi-

nences are present on the anterior margin). The pedal prints of *Agrestipus* (length, 150 mm; width, 110 mm) fall in the range of those of Morphotype C. The absence of manual prints is attributed to bipedality or to full overprinting (Weems, 1987). If *Agrestipus* is indeed a sauropod, Morphotype C could be regarded as a surviving member of a small, hitherto unrecognized sauropod lineage.

The second ichnogenus is *Tetrasauropus*, long interpreted as a prosauropod from the Late Triassic Chinle Group (upper part) of Colorado and New Mexico, but recently reinterpreted by Lockley et al., (2001) as a true sauropod, on the basis of track morphology (the podial print shape closely resembles that of *Brontopodus bairdii* Farlow, Pittman, and Hawthorne, 1989 from the Cretaceous of the Gulf Coast, but its size is much smaller), and the discovery of Late Triassic sauropod skeletal remains (Buffetaut et al., 2000). *Tetrasauropus* might be congeneric to *Tetrapodus/Tetrapodosaurus* from the Late Triassic of South Africa (Ellenberger, 1972, 1974); however, in the latter, size is larger (pes length range: >~440 mm vs. 200–300 mm in *Tetrasauropus*; Lockley et al., 2001:185), and the toes curve inwardly rather than outwardly, as in true sauropods.

Morphotype C approaches the lower end of *Tetrasauropus* size range, but differs from it in these features: (a) ovoid rather than subtrapezoidal podial prints, (b) antero-laterally rather than anteriorly directed toes, (c) less-developed toes, and (d) antero-posteriorly longer manual prints, with no digit impressions (they are shorter, more curved, and show well-developed digits in *Tetrasauropus*). These reasons show that Morphotype C and *Tetrasauropus* are diagnostically different. Both ichnogenera and *Agrestipus* seem to represent a sauropod lineage distinctly characterized by small size that thrived during the Late Triassic–Early Jurassic; its survival in the Middle Jurassic of southeastern Mexico (as represented by Morphotype C), probably was due to the peculiar ecologic/geographic setting there, as discussed below (see “Geographic, Ecologic and Biogeographic Considerations of the Xochitlapilco” section). Further, the presence of small sauropods in the Late Jurassic of Colorado, western North America (Lockley et al., 1986) lends support to the hypothesis on the post-Early Jurassic survival of this small sauropod lineage.

Hamanosauripus (Late Cretaceous Jingdong Formation, of Korea (Kim, 1986; Lim et al., 1995)) podial tracks are 330 mm long and ~200 mm wide, ellipsoid, with the anterior margin less curved than the posterior, and bearing three clawed toes, where the inner one is larger than the others. The manual prints are ovoid and show no digit impressions. Morphotype C is ~33% smaller than *Hamanosauripus*, differing from it in morphology (e.g., antero-laterally directed, clawless toes), geologic age, and geographic location, thus ruling out any close

relationships between their track makers. Further, Farlow et al. (1989) have questioned the validity of *Hamanosauripus*.

Also from the Jingdong Formation, Lim et al., (1989) figured but did not describe or name very small, undoubted sauropod tracks (length 185 to 195 mm), which differ in size and shape from those of *Hamanosauripus*, but closely resemble in shape those of *Brontopodus bairdii* from the Gulf Coast (cf. Lim et al., 1989:fig. 35.4 and Farlow et al., 1989:fig. 42.3). Hence by the Late Cretaceous, at least two kinds of small sauropods lived in Korea, and left footprints in the Jingdong Formation.

Possible Correspondence with Linnean Taxonomic Categories

By Middle Jurassic time, members of the first sauropod radiation (e.g. *Datosaurus* Dong and Tang, 1984 and *Klamelisaurus* Zhao, 1993, of China (Dong and Tang, 1984; Dong, 1992)) coexisted with members of the neosauropod radiation then underway (McIntosh, 1990, Sereno, 1999; Upchurch et al., 2004), such as *Omeisaurus* Young, 1939 and *Shunosaurus* Dong and Tang, 1984 of China (Young, 1939; Dong et al., 1983), *Cetiosaurus* Owen, 1841 of England (McIntosh, 1990; Glut, 1997) and *Lapparentosaurus* Bonaparte, 1986 of Madagascar (Bonaparte, 1986), all of which were far too large to include small sauropods as the trackmaker of Morphotype C. Hence it could be possible that the Morphotype C maker belongs to a hitherto unrecognized and undescribed suprageneric taxon of truly small sauropods, such as the track makers discussed above.

Geographic Distribution and Geologic Age

Middle Jurassic sauropod track published records are few and far apart: Australia: (Queensland (Molnar, 1991, seemingly a questionable record)); Europe: England (White Limestone Formation in Oxfordshire (Lockley and Meyer, 2000)), France (Dépt. de l'Indre (Farlow, 1993)), Portugal (Pedreira do Galhina site near Fatima (Dos Santos et al., 1994)); and North America: United States (New Mexico, Summer-ville Formation (Lockley et al., 1994; Lucas and Heckert, 2000)) and Mexico (Oaxaca (this report)). The Summerville tracks are much larger than those from Oaxaca.

It should be noted that the age and stratigraphic position of the Summerville Formation seem unsettled (cf. Gillette, 1996a and b for a review of the problem); however, according to S. Lucas (personal communication, Jan. 2005), the Summerville Formation includes strata of latest Middle Jurassic age and earliest Late Jurassic age, so it may be that the Summerville tracks are actually of Late Jurassic age. In any case, the Mexican tracks are older than the Summerville ones, and may be the oldest Jurassic record of sauropods in North America; in addition, they extend ~2,500 km

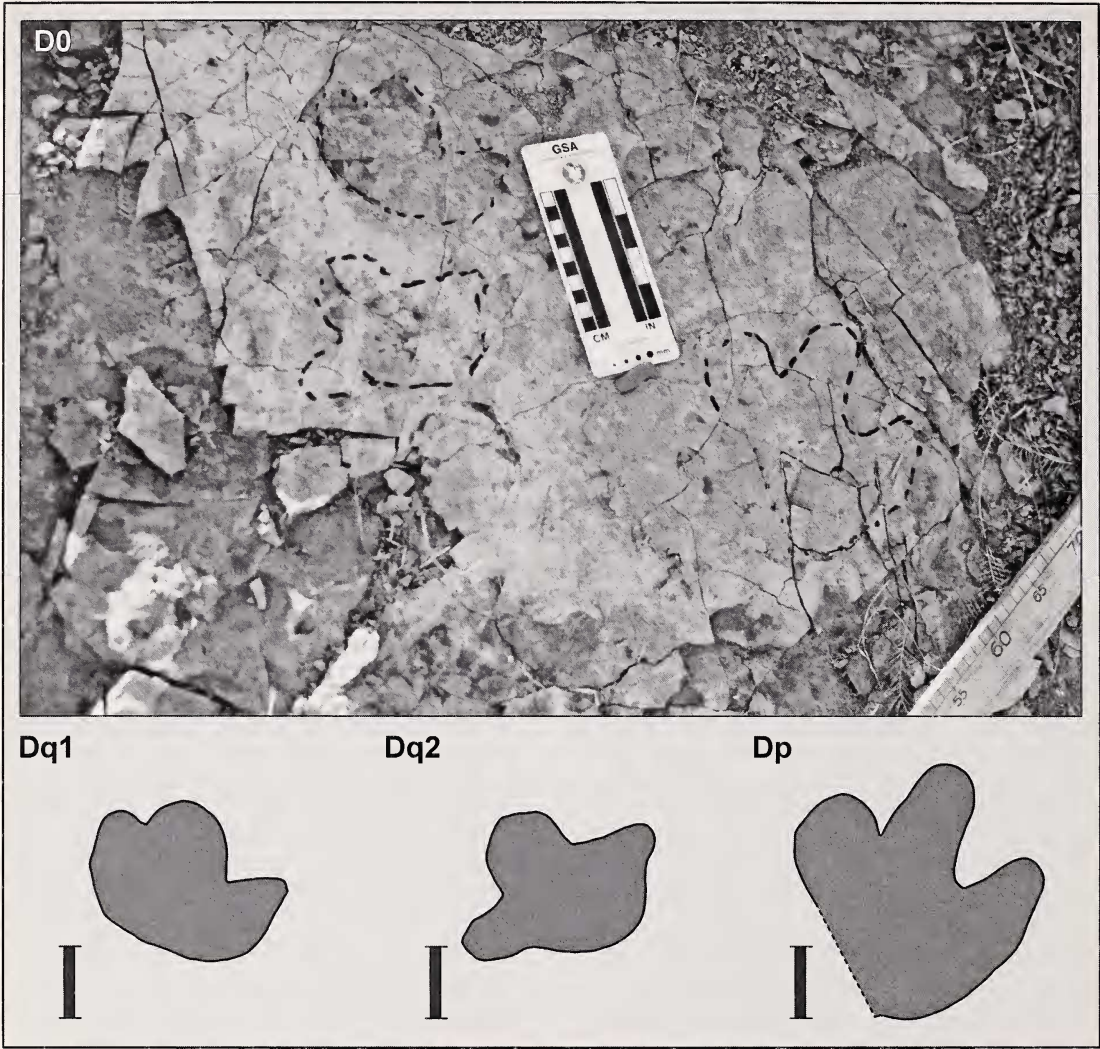


Figure 12 Morphotype D, small footprint assemblage originated by track makers referred to ?ankylopollexian ornithopods *sensu* Norman, 2004; D0, photograph of the small outcrop where footprints assigned to this morphotype are exposed; ruler indicates 10 cm; Footprint MVs Dp and Dq: Dp (f# 34, right), Dq1 (f# 36, right), and Dq2 (f# 35, indefinite), computer drawings of footprint silhouettes from IGM-7960, plastic sheet outline record of footprints exposed on the small outcrop depicted in D0; scale bar = 5 cm. (f# = footprint number)

southward the record of Middle Jurassic saur-
opods in this subcontinent.

- Order Ornithischia Seeley, 1888
- Suborder Cerapoda Sereno, 1986
- Ornithopoda Marsh, 1881
- Iguanodontia Sereno, 1986
- “Basal Iguanodontia” *sensu* Norman, 2004
- ?Ankylopollexia Sereno, 1986
- Morphotype D, Morphic Varieties Dp–Dq
(Figure 12, Table 6)

DESCRIPTION. Small, rounded to ovoid
footprints with short, wide, round-tipped digits.

Digit III is the longest, the other two are
subequal, with a total divergence angle close to
60°, and an estimated hip height of ~0.43 to
0.84 m; other measurements on Table 6. These
footprints are exposed on the same bedding
plane as those of the main outcrop located
~20 m east.

Morphic Variety Dp
REFERRED MATERIAL. IGM-7960, plastic
sheet, footprint number 34 (right, Figure
12Dp).
DESCRIPTION. This print is the best preserved
and provided the morphotypic characters. It
should be noted that the internal posterior margin
was not clearly preserved.

Table 6 Measurements of footprints assigned to Morphotype D ABBREVIATIONS: f#, footprint number recorded on IGM 7960; others as in Table 1. (A), Morphometric ratio method: $h = 4.8 \text{ fl}$ (Thulborn, 1989:251, Equation 8.4); (B), Allometric equation method: $h = 3.97 \text{ fl}^{1.8}$ (Thulborn, 1990:254, Equation 8.12). Linear measurements in mm

Atributes	f# 34	f# 35	F# 36
Side	R	I	R
MV	Dp	Dq2	Dq1
Fl	175	110	100e
fw	172	150	133
H (A)	840	528	480
H (B)	750	471	428
dIII	45	—	15
dwII	55	—	37
dIII	69	42	32
dwIII	55	58	65
dIV	50	—	33
dwIV	58	—	44
DA	57°	—	82°
ai II–III	28°	—	35°
ai III–IV	29°	—	47°

DISCUSSION. See the morphotype’s “General Discussion” below.

Morphic Variety Dq

REFERRED MATERIAL. IGM-7960, plastic sheet, footprint numbers 36 (right, Figure 12Dq1) and 35 (indeterminate, Figure 12Dq2).

DESCRIPTION. Short prints with widely based short digits, having a total divergence angle of 80° to 100°.

DISCUSSION. The shape of these footprints differs from that of MV Dp in being relatively shorter and wider, as well as in having shorter and wider digits; however, it should be noted that these footprints are less well defined than footprint 34 (the only MV Dp); this in turn suggests that deficient printing may account for the shape differences, particularly so for the virtual lack of the digit II and IV impressions in footprint 35. The latter and footprint 36 are actually smaller than footprint 34 (their width is 13%–22% smaller than that of footprint 34), this size difference may represent sex, individual, or age variation. However, it seems most probable that the smaller footprints were made by juvenile individuals.

GENERAL DISCUSSION OF THE MORPHOTYPE

Morphotypic Assignment

In spite of the differences mentioned above, these footprints show an overall similar morphology, which indicates that their track makers belonged to the same population, and are therefore assigned to the same morphotype.

Ichnological Assessment: Introductory Remark

The size and morphology of the footprints assigned to Morphotype D are those of small ornithopods (Thulborn, 1990; Lockley, 1991b, Leonardi, 1994). Thulborn (1990) characterized such footprints as being tridactylar, mesaxonic, with digits II and IV subequal, slightly divergent; digit IV is smaller, 20 to 25 cm anterior-posterior length range and a total divergence angle around 60°. Other criteria include tracks as wide as (or wider than) long, toes without claws or with little-developed claws, lack of hallux impression, lack of plantar notch (cf. Haubold, 1971, 1984). It should be noted though, that still all these criteria are not universally followed (cf. Olsen and Baird, 1986).

Although the preservation of Morphotype D tracks is moderate to poor, they show most of the features listed here as characteristic of those attributed to small ornithopods, namely being nearly as wide (or wider than) as long, tridactylar, mesaxonic, with subequal digits II and IV, digit IV smaller, absence of claws, and lack of plantar notch. Thus they could not be extramorphological variants of small theropods, that is, tracks whose shape and diagnostic features greatly depart from those of the typical or characteristic track morphology attributed or known to belong to a given track maker (concept proposed by S. Lucas, personal communication, July 2005); rather, Morphotype D tracks are clearly eomorphic (i.e., preserved well enough to allow detection of their shape and other diagnostic features; it is the antonym of the previous concept), and readily attributed to small ornithopods.

Ichnogeneric Summary Review

Formally named Jurassic ornithopod ichnogenera are not numerous; among the better-known ones are *Anomoepus* Hitchcock, 1848, *Dinehichnus* Lockley, dos Santos, Ramalho, and Galopin, 1993, *Gyrotrisauropus* Ellenberger, 1972, *Gypsichnites* Stenbergl, 1932, *Iguanodon* Mantell, 1825, *Jialingpus* Zhen, Li, and Zhen, 1983, *Pseudotrisauropus* Ellenberger, 1972, and *Sinoichnites* Khun, 1958. Perhaps more than in any other group, the morphological and size diversity displayed by the footprint record has made it quite difficult to characterize and relate taxa. For instance, within the named ichnogenera, there are forms such as *Anomoepus* and *Jialingpus*, characterized by small size and narrow toes, thus resembling *Grallator*; they contrast with forms such as *Gypsichnites*, *Gyrotrisauropus*, and *Iguanodon*, characterized by medium to large size, and medium to broad toes, with pointed to rounded tips. Another complicating matter is the unsettled formal taxonomic and nomenclatorial status of some ichnogenera, so before making comparisons, a few comments are put forward.

Several species of *Grallator* have been transferred to *Anomoepus* (cf. Haubold, 1971). Pitt-

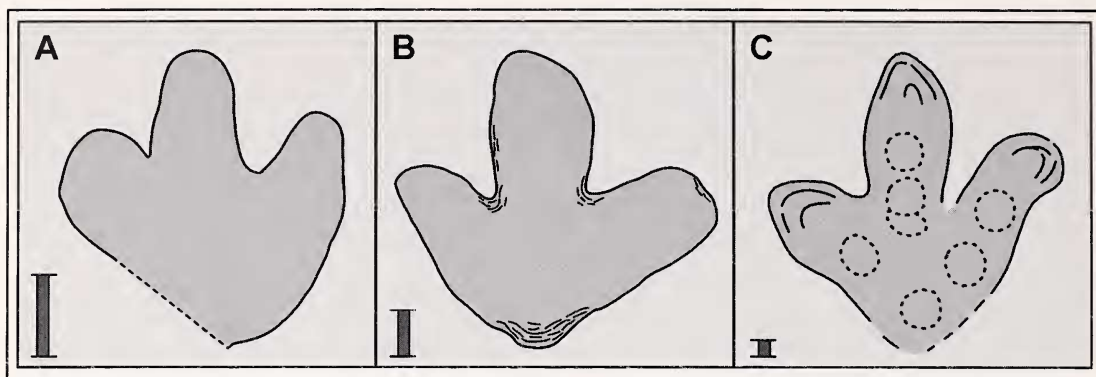


Figure 13A–C Ichnological comparison of Morphotype D with *Sinoichnites* and *Gyrotrisauropus*. Prints are adjusted to the same size to ease comparisons; scale bar = 5 cm; A, footprint #34 of IGM-7960, a right pedal print assigned to MV Dp; B, *Sinoichnites youngi* Kuhn, 1958 from the Middle Jurassic of China. (Redrawn from Haubold, 1971:fig. 54.10; and Zhen et al., 1989:fig. 19.2E); C, *Gyrotrisauropus* Ellenberger, 1972 from the Early Jurassic of South Africa. (Redrawn from Thulborn, 1990:fig. 6.33b)

man (1992) proposed a different course: *Grallator* should include as junior synonyms *Anomoepus* and *Gypsichnites*, because they share most character states of *Grallator*. Further, given the close resemblance and geologic age between *Anomoepus* and *Jialingpus*, there is a real possibility that both taxa be congeneric, hence *Jialingpus* could be a junior synonym of *Anomoepus*. *Hoplichnus* Early Jurassic of Arizona (Welles, 1971) is another example of the ‘provincial taxonomy’ approach, and is considered a junior synonym of *Anomoepus* by Lockley and Hunt (1995:122). At any rate, the resolution of these and related problems lies beyond the scope of the present paper, so in the following comparison of Morphotype D with the named ichnogenera, we shall make comments to express our position on some problematic taxa.

Morphotype D tracks are slightly larger than those of the nearly ubiquitous *Anomoepus* (Late Triassic of eastern North America (Lull, 1953; Olsen, 1980; Olsen and Baird, 1986), southwestern North America (Texas and New Mexico, Murry, 1986; Clark and Fastovsky, 1986), Early Jurassic of eastern North America (Olsen and Sues, 1986), and Europe and South Africa (Haubold, 1971, 1986)). Olsen and Baird (1986) synonymized *Moyenisauripus* (Early Jurassic of South Africa (Ellenberger, 1972)) with *Anomoepus* on the basis of size and strong overall resemblance; this change has been accepted (cf. Haubold, 1986). Lockley and Hunt (1995) have synonymized *Hoplichnus* (Early Jurassic of Arizona, Welles, 1971) to *Anomoepus* also on the basis of size and strong overall resemblance. Both moves are followed here. *Jialingpus* (Early Jurassic of China, Zhen et al., 1983) is also very similar in size and morphology to *Anomoepus* (cf. Zhen et al., 1989:figs. D and E, the only difference

between these ichnogenera is the shape of the metatarsal impression); therefore we include *Jialingpus* within *Anomoepus*. Morphotype D tracks also differ from *Anomoepus* tracks in being nearly as wide as (or wider than) long, with short, stout toes displaying a large divergence angle; the pads are poorly (if at all) developed, and the plantar region is wider; the metapodial impression frequently present in *Anomoepus* tracks is absent in Morphotype D.

Morphotype D tracks are about the same size that those of *Apatichnus* (Early Jurassic of eastern North America (Lull, 1953)), but differ from them in being much wider, with short, stout toes, which display a greater divergence angle. Morphotype D tracks are ~30% larger than those of *Atreipus* (Early Jurassic of eastern North America (Olsen and Baird, 1986)). According to these authors, *Atreipus* includes species of *Gigandipus* (same age and provenance, Bock, 1952), and of *Anchisauripus* (same age and provenance, Bock, 1952). Here we have partly followed their interpretation (see our ichnogenetic assessment of Morphotype A). Morphotype D tracks differ from *Atreipus* tracks in being wider (width may be greater than length), with short, stouter toes, which display much a greater divergence angle. It should be noted that *Atreipus* has also been interpreted as made by a theropod, and as such it was discussed in Morphotype A.

Morphotype D tracks are less than half as long as those of *Gypsichnites* (Early Jurassic of South Africa (Ellenberger, 1972)), but differ from them in being wider (length:width ratio 175:172 mm vs. 450:290 mm in *Gypsichnites*) and in having short, stout, round-tipped toes which display a greater divergence angle; further, digit III in Morphotype D is straight and shorter than in *Gypsichnites*, which is longer and slightly curved.

Morphotype D tracks are less than half as long as those of *Gyrotrisauropus* (Early Jurassic of South Africa (Sternberg, 1932; Ellenberger, 1972; Thulborn, 1990)), but the shape shows some resemblance; both are wide tracks with short, stout, round-tipped toes, which display a large divergence angle (Figure 13). Unlike *Gyrotrisauropus*, Morphotype D tracks show no pads.

Morphotype D tracks are less than half as large as those of '*Iguanodon*' (Late Jurassic of England (Sarjeant, 1974)), and also differ from them in having short, stout, and round-tipped toes. Morphotype D tracks are 40% smaller than those of *Pseudotrisauropus* (Early Jurassic of South Africa (Ellenberger, 1972)), and differ from them in having toes with a wider basal part that tapers distally, whereas in *Pseudotrisauropus*, the wider part is subdistal; also in Morphotype D, the interdigit II–III cleft is much shallower than in *Pseudotrisauropus*.

Morphotype D tracks are ~40% to 50% smaller than those of *Sinoichnites* (Late Jurassic of China (Kuhn, 1958; Young, 1960; Haubold, 1971, 1984; Zhen et al., 1983, 1989)), but show an overall resemblance (Figure 13) in shape (wide tracks with short, stout toes, shallow interdigit cleaves) and divergence angle (large). Morphotype D tracks significantly differ in size and shape from the putative ornithopod ichnogenera *Yangtzeopus* (early Late Jurassic of China (Young, 1960; Kuhn, 1963; Haubold, 1971, 1984)) and *Youngichnus* (Early Jurassic of China, (Zhen et al., 1989)), also interpreted as a theropod track (Zhen et al., 1989)).

In conclusion, Morphotype D significantly differs in size and morphological features from the ichnogenera discussed, although it shows some shape resemblance to *Gyrotrisauropus*, and more so to *Sinoichnites*; however, the limited material basis of Morphotype D, plus the size and geologic age differences, as well as the enormous geographic separation between this morphotype and both *Gyrotrisauropus* and *Sinoichnites*, lead us to regard it as not congeneric with either ichnotaxon.

Possible Correspondence with Linnean

Taxonomic Categories

By Middle Jurassic time, basal ornithopods (Euornithopoda Sereno, 1986, Hysilophodontidae included (cf. Sues, 1997a and b; Sues and Norman, 1990)) have succeeded the Late Triassic–Early Jurassic heterodontosaurid (Weishampel and Witmer, 1990; Smith, 1997) and basal thyreophoran ornithischians (Weishampel, 1990, 2004; Dong, 1992; Glut, 1997); known only from China, they include *Yandusaurus* He, 1979, *Gongbusaurus* Dong et al., 1983, and *Agilisaurus* Peng, 1990 (and 1992); they were gracile, small, cursorial, tridactylar digitigrade dinosaurs; their feet had long, slender metatarsals; long, delicate digits; and pointed to rounded unguals; digits II

and IV slightly diverged from digit III. This foot structure would have produced long and narrow tracks quite different from Morphotype D.

By default, the possibility that the Morphotype D track maker was an iguanodont merits consideration. As previously discussed, this morphotype closely resembles tracks commonly attributed to iguanodonts (cf. Thulborn, 1990; Lockley and Meyer, 2000). Further, in size Morphotype D corresponds to tracks that could have been made by a medium-size iguanodont, like the Late Jurassic North American *Dryosaurus* (cf. Galton, 1981; Glut, 1997; Ryan, 1997); in shape, because of its short, blunt, divergent digits, Morphotype D approaches the condition seen in tracks attributed to much larger iguanodonts, like the Early Cretaceous *Iguanodon* (Norman and Weishampel, 1990; Sarjeant et al., 1998; Lockley and Meyer, 2000); the well-known ankylopollexian *Camptosaurus* from the Late Jurassic of North America and Europe (Glut, 1997; Norman, 2004) has already ponderous feet with short, stocky digits (cf. Glut, 1997:247), that could have produced tracks not unlike Morphotype D, save that digit IV would be less divergent. Under these circumstances, it appears more parsimonious to hypothesize that the Morphotype D track maker probably was a Middle Jurassic early ankylopollexian iguanodont, as yet unrecorded in bone. The discovery of Late Triassic sauropod bone remains (Buffeteau et al., 2000), long suspected on the basis of tracks, and lends support to this possibility (cf. Lockley et al., 2001).

Geographic Distribution and Geologic Age

Jurassic small ornithopod footprint published records are rather scarce: Early Jurassic: North America (Portland Formation of the Connecticut Valley (Lull, 1953; Olsen, 1980; Olsen and Sues, 1986); Kayenta Formation of southwestern United States (Welles, 1971; Lockley and Hunt, 1995)), Europe: Poland (Swietokrzyskie Mountains (Karaszewski, 1969)), Germany (southern region (Haubold, 1971, 1984)), South Africa: Lesotho (Upper Elliot Formation (Sternberg, 1932; Ellenberger, 1972, 1974; Thulborn and Wade, 1984)), and South America: Brazil (Sao Paulo, Botucatu Formation (Leonardi, 1994)). Middle Jurassic: Europe: Scotland (Lealt Shale (Andrews and Hudson, 1984)). Late Jurassic: North America: Mexico (Michoacán (hysilophodontid tracks, Ferrusquía-Villafranca et al., 1978)), Europe: England (southern region (Sarjeant, 1974)), China (largely the Sichuan Province (Kuhn, 1958, 1963; Young, 1960; Haubold, 1971, 1984; Zhen et al., 1983, 1989)). The tracks from Oaxaca, southeastern Mexico extend ~3,000 km southward the record of Middle Jurassic small ornithopods in North America.

GEOGRAPHIC, ECOLOGICAL, AND BIOGEOGRAPHIC CONSIDERATIONS OF THE XOCHITLAPILCO DINOSAUR ICHNOFAUNA AND ITS ENVIRONMENT

Recent models of the Mesozoic geologic and tectonic evolution of the southeastern Mexico–middle American region (Figure 5), portray the Mixteca territory (also known as the Mixteca Terrane), as one of the several small continental-crust blocks set in the widening space between North America, Africa, and South America, as Pangea became disassembled. Paleogeographically, such blocks would have been islands; however, there are not sufficient data to constraint the sea/land boundary of any one block during the Jurassic and most of the Cretaceous. Regardless of the model, the Mixteca territory would have been a Middle Jurassic island, probably of small size, still lying close to North America, South America, and Africa (Figure 5).

The diversity of this ichnofauna, given the reduced number of tracks and the small outcrop area where they occur, is indeed noteworthy. The fact that three of the four track makers were small dinosaurs, two herbivorous (one sauropod and an ankylopollexian ornithopod) and one carnivorous (a “basal coelurosaur” theropod), appears to be not merely coincidental, and calls for an explanation; we offer as such this speculation: The Xochitlapilco dinosaurs belonged to a community set in a restricted and/or isolated scenario, where limited space and resources would have induced selective pressures toward small size, particularly to the primary consumers (i.e., the herbivores), and to their associated predators (the “basal coelurosaur”). Larger predators such as the allosauroid recorded by the Morphotype B footprint, could survive in a setting like this, having much lower population densities than the small dinosaurs; hence their representation in the ichnofauna would be lesser than that of the small forms. The paleogeographic island scenario proposed above, although conjectural, would provide the environmental setting required for this ecological hypothesis. In addition such a scenario would be consistent with the idea that the fauna was shielded from competition and exchange with continental faunas, thus promoting its endemic condition and peculiar physiognomy.

Finally, given the supposed location of the Mixteca block during the Middle Jurassic (Figure 5), one would expect some overall biogeographic/phylogenetic resemblance of the Xochitlapilco dinosaur fauna with coeval faunas from North America, South America, and Africa. To test this hypothesis, Table 7 was prepared; it is a compilation of pertinent taxonomic/distributional data for these and other continents. It discloses that the Xochitlapilco fauna shows greater resemblance to the North American fauna and to the Northern Hemisphere Chinese and

Western European faunas than to the Southern Hemisphere, Gondwanic South American, African, and Australian faunas. However, the Xochitlapilco fauna is too small to objectively assess the validity of this resemblance.

SUMMARY AND CONCLUSIONS

1. The Xochitlapilco Dinosaur Ichnofauna was recovered from steep outcrops of thinly bedded, red, phyllarenitic, fine-grained sandstone and shaley siltstone belonging to the Tecocoyunca Group *partim*, which was laid down in a tropical coastal lagoon, and dated as Early Bajocian–Early Bathonian on the basis of ammonites. The site lies in the Oaxacan Mixteca, southeastern México.
2. The ichnofauna mainly consists of small footprints, whose makers are referred to a “basal coelurosaur” (Morphotype A tracks), an undescribed eusauropod taxon, probably of family rank (Morphotype C tracks), and an ankylopollexian ornithopod (Morphotype D tracks); there is also a single large footprint, made by an ?allosauroid carnivorous. The scant material record of this fauna makes noteworthy its relatively high diversity.
3. The Xochitlapilco ichnofauna is the southernmost record of Jurassic dinosaurs in North America, and adds a new fauna to the meager record of dinosaurs in Middle America.
4. Middle American plate tectonics models of geologic/tectonic evolution portray the Mixteca territory ($\approx$ Mixteca Terrane), for the Jurassic, as one of the several small, continental-crust blocks laid in the inter-American/African space as Pangea became disassembled.
5. Ecologically, this paleogeographic scenario would have been an isolated setting, where limited space and resources might have imposed selective pressures toward small size, particularly to the primary consumers and associated predators. Such a setting would have shielded the island fauna from competition and exchange with neighboring continental faunas, thus promoting its endemic condition and identity.
6. Nonetheless, the Middle Jurassic Xochitlapilco dinosaur fauna shows a closer biogeographic/phylogenetic resemblance to the North American fauna than to the South American or African ones; however, the meaning of this fact can not be fully assessed at present, because of the Xochitlapilco fauna’s small size.

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Table 7 Selected dinosaur distribution/age data organized to disclose the biogeographic resemblance of the Xochitlapilco Dinosaur Ichnofauna, Middle Jurassic of southeastern Mexico. **ABBREVIATIONS:** Ltht, large theropod tracks; **MJROR**, Middle Jurassic dinosaur record based on osseous remains; co-occurring major taxa are counted individually; **MJRT**, Middle Jurassic dinosaur record based on tracks; co-occurring small, medium size and/or large tracks are counted individually, because each class size-track is interpreted as made by dinosaurs that belonged to a particular Linnean major taxon. **MphA to MphD**, Morphotypes A to D respectively; **TMJR**, total Middle Jurassic dinosaur record. Middle Jurassic record data in bold type. (Chief sources, osseous remains: Bartholomai and Molnar, 1980; Dong et al., 1983; Dong and Tang, 1984; Milner and Norman, 1984; Rowe, 1989; McIntosh, 1990; Weishampel, 1990, 2004; Dong, 1992; Currie and Zhao, 1993; Zhao and Currie, 1993; Upchurch, 1993; Glut, 1997, 2000, 2002, 2003; Holtz et al., 2004; Norman, 2004; Upchurch et al., 2004). (Chief sources, tracks: Young, 1960; Casamiquela, 1964; Haubold, 1971, 1984; Ellenberger, 1972, 1974; Sarjeant, 1974; Ferrusquía-Villafranca et al., 1978; Zhen et al., 1983, 1986, 1989; Demathieu, 1989; Thulborn, 1990; Leonardi, 1994; Lockley and Hunt, 1995; Lockley et al., 1986, 1996a–b, 2001; Lockley and Meyer, 2000)

Type of record	North America				Europe			Africa			South America	
	South and Southeastern		Western North America		Asia		Continental Europe		South Africa		Australia	
	Mexico				China		United Kingdom				Queensland	Brazil, Argentina, and Chile
Osseous remains	—	Late Jurassic/Coelurosauria incert. sed.			—		Middle Jurassic/Coelurosauria incert. sed.	—	?	Late Jurassic/Coelurosauria incert. sed.	—	—
Tracks	Late Jurassic/Coelurosauria incert. sed. Middle Jurassic/MphA: small tracks: “Basal-Coelurosauria”	Middle Jurassic/small theropod tracks Early Jurassic/small theropod tracks		Middle Jurassic/small theropod tracks Early Jurassic/small theropod tracks			Middle Jurassic/small theropod tracks Late Triassic/small theropod tracks	Middle Jurassic/small theropod tracks	Early Jurassic/ small theropod tracks	Middle Jurassic/ small theropod tracks	Middle Jurassic/ small theropod tracks; Early Jurassic/medium-size and small theropod tracks	—
Osseous remains	—	Late Jurassic/Allosauridae		Middle and Late Jurassic/ Sinraptorid Allosauridae, Carnosauria, Tetanurae incert. sed.			Middle Jurassic/ Tetanurae incert. sed.	Middle Jurassic/ Tetanurae incert. sed.	—	—	—	—
Tracks	Late Jurassic/Allosaurid tracks Middle Jurassic/MphB: large tracks: ?Allosauridae	Late Jurassic/Ltht Middle Jurassic/ large theropod tracks Early Jurassic/Ltht		Middle Jurassic/ large theropod tracks; Early Jurassic/ medium-size theropod tracks			Middle Jurassic/ large theropod tracks	Late Jurassic/ large theropod tracks	—	Early Cretaceous/ large theropod tracks	—	Late Jurassic/ large theropod tracks
Osseous remains	—	Middle Jurassic/Basal Sauropoda”, Diplodocidae incert. sed.		Middle Jurassic/ “Basal Sauropoda”, “Basal Eusauropoda”, Basal Neo-sauropoda”, Macronaria			Middle Jurassic/ Cetiosauridae, Diplodocidae	Middle Jurassic/ Eusauropoda incert. sed. Diplodocida incert. sed.		Middle Jurassic/ “Basal Sauropoda”	—	Late Middle Jurassic/ “Basal Sauropoda”, “Basal Eusauropoda”, Cetosauridae
Tracks	Middle Jurassic/MphC: small tracks: undescribed sauropod family	Middle and Late Jurassic/small sauropod tracks; Late Triassic/small sauropod tracks					Middle Jurassic/ medium to large sauropod tracks	Late Jurassic/ large sauropod tracks Middle Jurassic/ medium to large sauropod tracks	Middle Jurassic/ medium to large sauropod tracks	—	—	—

Table 7 Continued

Type of record	North America			Europe		Africa		South America	
	South and Southeastern Mexico	Western North America	Asia	United Kingdom	Continental Europe	South Africa	Australia	Brazil, Argentina, and Chile	
Osseous remains	—	Late Jurassic-Early Cretaceous/Iguanodontidae; Late Jurassic/Euornithopoda, Ankylopollexia, Dryosauridae	Middle Jurassic/Euornithopoda; Early Cretaceous/Iguanodontidae	Early Cretaceous/Iguanodontidae	Early Cretaceous/Iguanodontidae; Late Jurassic/Euornithopoda, Ankylopollexia	Early Jurassic/Heterodontosauridae	Early Cretaceous/Euornithopoda	—	
Tracks	Late Jurassic/Thyrsilophodontid tracks	Early Jurassic/small ornithopod tracks	Late Jurassic/medium-size ornithopod tracks; Early Jurassic/large and small ornithopod tracks	Late Jurassic/large ornithopod tracks	Middle Jurassic/small ornithopod tracks; Early Jurassic/small and medium-size ornithopod tracks	Early Jurassic/large and small ornithopod tracks	—	Early Jurassic/small ornithopod tracks	
MJOR	0	1	8	3	3	0	1	3	
MJRT	4	3	2	4	4	2	0	0	
TMJR	4	4	10	7	7	2	1	3	

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